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## JUVENILE KELPS AND THE RECAPITULATION THEORY. I.

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### I. THE DEVELOPMENT OF CERTAIN KELPS

#### A. *Renfrewia*<sup>1</sup>

For the preparation of a former article (Griggs, '06) on *Renfrewia* the writer had no very young plants, but during the summer of 1907 he was enabled to collect a full series at the Minnesota Seaside Station, Port Renfrew, B. C. This material is of interest for the study of the development of this, the most primitive of the kelps in comparison with the more complex forms.

The smallest specimen found, which measures a trifle less than 4 mm. (Fig. 1), is not certainly determinable. But one 13 mm. long (Fig. 2) had already developed a peculiar swelling of the basal region which characterizes the young plants. The primitive disc of most kelps and of *Renfrewia* up to this age is rather flat and sharply separable from the stipe, which ascends cleanly without tapering from the top of the disc. In *Renfrewia*, however, the basal region of the stipe (the region which in other kelps develops hapteric outgrowths) increases in size. As the plant grows this swollen region becomes more prominent till in plants 8 cm. long (Fig. 11) the

<sup>1</sup> Since publishing the original account of *Renfrewia parvula* in 1906 I have found that it is apparently conspecific with Setchell's ('01) *Laminaria ephemera* earlier described from the California coast. Accordingly Setchell's name replaces mine and the plant becomes *Renfrewia ephemera* (Setchell). Cf. Setchell, '08 b.

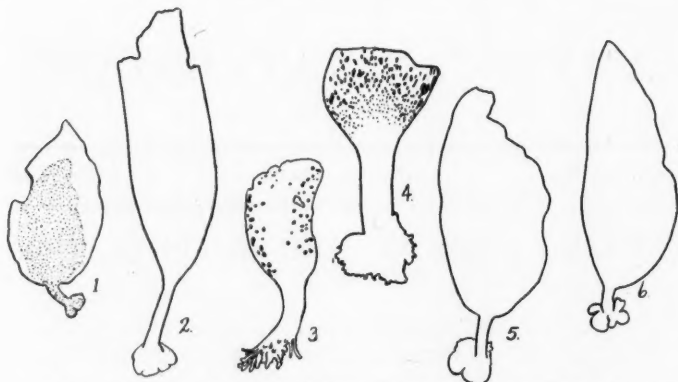


FIG. 1. *Renfrewia*, 4 mm., shading shows the position of single and many-layered areas in the lamina, holdfast without basal cone.

FIG. 2. *Renfrewia*, 13 mm., lamina many-layered throughout basal cone beginning to appear.

FIG. 3. *Lessoniopsis*, 1.1 mm., lamina about four-layered, spots already shown in the cortex, holdfast not developed, plant apparently anchored by filaments.

FIG. 4. *Lessoniopsis*, 2.3 mm., spots in the lamina larger and more evident distally, but still small near the transition region, indicating that growth is already localized, primitive disc developing at base of stipe.

FIG. 5. *Hedophyllum*, 2.3 mm., showing the much-lobed primitive disc.

FIG. 6. *Hedophyllum*, 10 mm., lobes of primitive disc grown into the primitive hapteres.

holdfast is an almost straight-sided cone 5 mm. in diameter and of about equal height. Though apparently insignificant this character makes it easy to pick out *Renfrewia* from other kelps while yet very small. So far as the writer is aware it is not present in any other kelp.

After the plant has reached about a decimeter in length the basal cone ceases to increase and later is lost in the growth of the stipe (Fig. 12). At the same time the disc begins to enlarge and spread out on the substratum, giving a firmer hold for the increasing lamina above. This enlargement is clearly in the region of the primitive disc and not in the conical basal swelling above, which remains part of the stipe. These two tendencies of growth working together usually cause the sharp distinction between the holdfast and stipe to reappear, and in plants more than 15 cm. long the conical base is seldom prominent (Fig. 13). In adults the disc becomes very flat and thin by its continued extension (Fig. 14).



FIGS. 7-11. *Renfrewia*, series of young plants showing the development of the basal cone. Four fifths natural size.

FIGS. 12-13. *Renfrewia*, older plants showing the gradual disappearance of the basal cone with increase in size. Four fifths natural size.

FIG. 14. *Renfrewia*, base of an adult plant, fruiting area extending over almost the entire lamina, its margin indicated by shadows here and there, hold-fast showing primitive hapteres. Four fifths natural size.

Some speculations as to the nature and significance of this cone may be of interest. Of all the kelps *Renfrewia* and *Cymathere* are the only ones in which the mature holdfasts are restricted to the primitive disc region. In the development of the latter genus, as traced by the writer ('07), there is no indication of such an organ as can be seen by an inspection of the figures then published. *Phyllaria* and *Saccorhiza* differ in their holdfast characters from all the other genera. Instead of putting out hapteres directly from their stipes they develop bulbous "rhizogens" which form ring-like collars around the stipe. From these the hapteres are formed by unequal growth along their margins. Though the rhizogen in both genera is separated from the primitive holdfast by a distinct interval on the stipe, it is essentially similar to the basal cone of *Renfrewia* which we may consider as an incipient rhizogen. This would indicate some leaning of *Renfrewia* toward the *Phylariatæ*; but its paraphyses are of the typical clavate form not at all similar to the linear ones of that group. Whether this basal cone is a nascent organ representing the beginning of the holdfast or is a vestige of a *Saccorhiza*-like rhizogen is a puzzling problem. At some stage in their history the rhizogens of *Saccorhiza* and *Phyllaria* probably passed through this condition and remained for a longer or shorter period without further development. On the other hand, the obscuring of the cone in *Renfrewia* when adult might suggest a vestigial organ. Perhaps the best hypothesis is that *Renfrewia* was cut out from the main advancing phylum of the kelps, isolated and fixed, at the stage where the tendency to form a secondary holdfast was just beginning to manifest itself.

The tissues of the many-layered lamina of *Renfrewia* are apparently acquired after the fashion of other kelps, but in *Renfrewia* the many-layered lamina begins its development in smaller plants than in the *Phylariatæ* including *Cymathere*. Even in the smallest specimen (Fig. 1) there is only a small portion of the one-layered blade remaining around the edge of the lamina. In the

13 mm. specimen (Fig. 2), the whole lamina is many layered without any signs of the one-layered portion persisting around its edges. Apparently the embryonic lamina is almost wholly transformed into the adult blade. Like the adult, these young plants are light colored and delicate in texture. They are narrowly elliptical in shape, cuneate at the base and rounding to the apex when not badly abraded.

Except for the basal cone of the stipe young plants 15 mm. long in all characters are like the adult. The adult is larger but the proportions remain the same. Even in the histology there is probably very little difference, for, as described below, *Renfrewia* develops very imperfectly the complex tissue system which characterizes the higher kelps. What differentiation of tissues appears is probably present long before adult size is reached. Were it not for their reproductive maturity it would be difficult to demonstrate that the adults were mature and not merely larger juvenile forms (Figs. 16, 17); and they have been mistaken by competent observers for juvenile forms of some other kelp.

#### B. *Lessoniopsis*

*Lessoniopsis* is a monotypic genus ranging along the Pacific coast from California to Vancouver Island. It was founded by Reinke ('03) to receive *Lessonia littoralis* Farlow and Setchell (see Setchell, '03) which differs from *Lessonia* in the marked dimorphism of the laminae, as described below.

The juvenile forms of *Lessoniopsis* are extremely abundant during July and August at the Minnesota Seaside Station. They grow in clumps of many individuals of all ages. As often as not these clumps start upon the stipes of other kelps, so that one can obtain many hundred specimens simply by cutting off a few old *Laminaria* stipes. Though the mature plants are often single, it is not at all unusual to find several large plants fused together, as was noticed by Reinke. The reason for this habit of growth of the sporelings is a matter of some in-

terest. There is no difference, as far as the writer is aware, between the fruiting habits of this and other kelps. In quiet water the fragments of any fruiting lamina torn off by the waves might lie undisturbed on the bottom and the spores might germinate close to the point of liberation. But this kelp is a cumaphyte growing exclusively in the strong surf, and it is in surf-scoured situations that the young plants are found best developed. This would lead one to look for some method of basal branching or possibly budding of new laminae from the holdfast, as is known in a few kelps which have "rhizomes." But though hapteres and stipes are occasionally so completely grown together as to appear branches of one plant, no evidence of such branching in the young plant has been observed and the writer must conclude that the clusters are due to starting of many spores at one point.

The young plants forming these clumps are thickly splashed with checks of dark brown on the lighter color of the body of the lamina. This is most conspicuous in plants about 10 cm. long and is clearly brought out in the photographs (Figs. 15, 21). As they grow older the spotting tends to disappear, but traces of it can usually be found in specimens of any age. No other kelp of the region is similarly marked except *Pterygophora*, in which the spots when present are much less distinct. As this appearance arises very early it is of the utmost service in identifying the plants while yet too young to have developed any characters of the adult.

The smallest specimen found (Fig. 3) measured about 1.1 mm. in length. It was attached to the hapteres of another plant of the same species twenty or thirty times as long. When loosened from its hold it came away with a mass of filamentous material which completely enveloped its base. In this tangle there was a considerable portion of foreign matter; but the appearance of the finer strands was that of a protonema-like felt organically connected with the young kelp which seemed to spring from it like the gametophore of a moss. On teasing this away it was seen that the primitive disc had not yet developed.

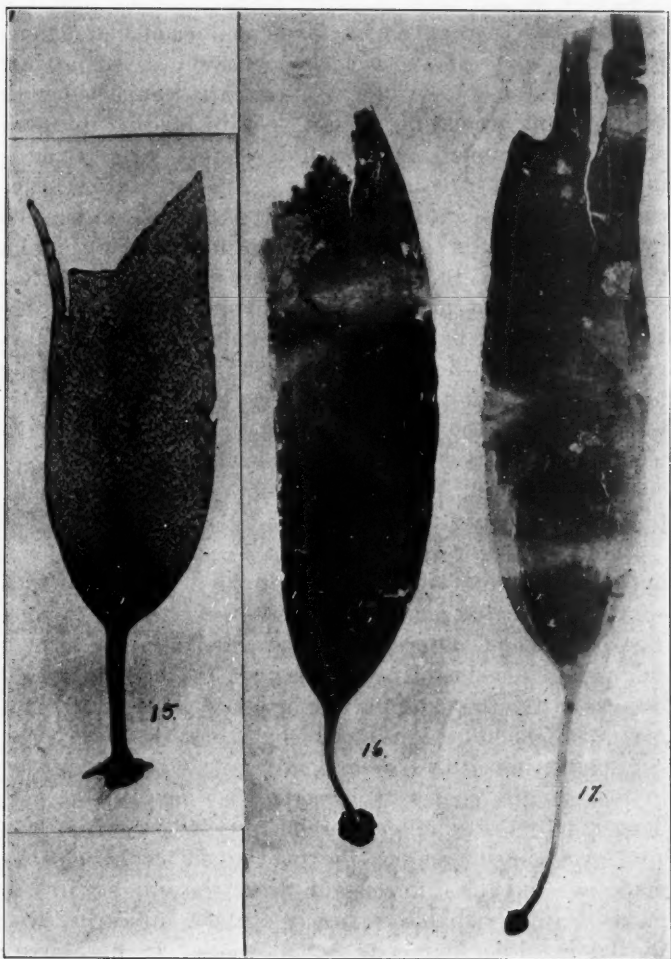


FIG. 15. *Lessoniopsis*, 30 mm., lamina showing the characteristic spots, midrib just beginning to appear, holdfast formed by conspicuous primitive hapteres.

FIGS. 16-17. *Renfrewia*, adult, showing similarity to *Lessoniopsis* when young, fruiting area covers almost the entire lamina in Fig. 16, but in Fig. 17 occupies only a small area at the base and hence clearly discernible, spots in Fig. 16, due to epiphytic algae. About one half natural size.

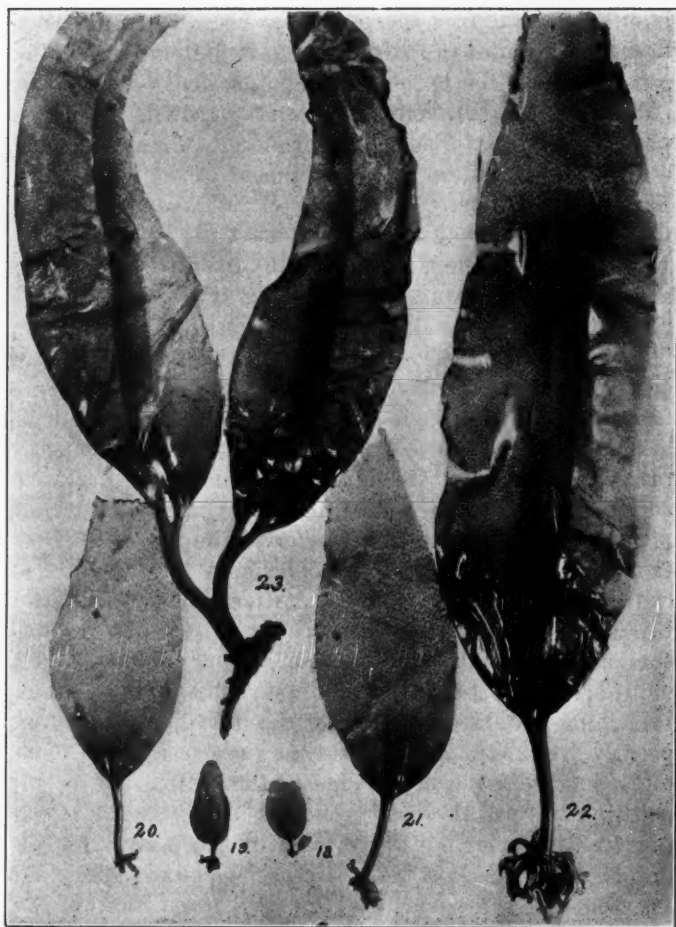
The base of the stipe was but slightly larger than the portion above and gave off a large number of filamentous processes, some of which seem to have pressed against the substratum, while others apparently connected with the filaments around the base. Notwithstanding its small size this specimen had a well-developed stipe about a dozen layers of cells in thickness. The internal cells are considerably elongated, though not, as far as can be seen by focusing, differentiated into a pithweb. The lamina was already several cells in thickness even at the edge. Since it was but little frayed, it hardly seems possible that there could have been any remnant of the one-layered lamina which had not been transformed into the many-layered adult blade. In this respect *Lessoniopsis* would stand at the opposite extreme from *Cymathere*, in which a large portion of the embryonic lamina is not changed, but continues to grow and persists until the plant is more than 20 cm. long.

The next larger specimen (Fig. 4) measures 2.3 mm., but its true length must have been about 5 mm., for it is sharply truncated a little above the base of the lamina. The holdfast of this specimen was enlarged to form a fairly well developed primitive disc, the base of which was, as in the first specimen, more or less imbedded in a mass of filaments apparently belonging to the kelp. The lamina was much thicker and the spots were seen to be in two layers, one on each side, just beneath the epidermis. In the smaller specimen (Fig. 3), where one spot overlapped another, the two layers could also be made out, but the difference in focus was so slight as to make it appear that they lay in contact, indicating that the lamina was four cells in thickness. In the larger specimen they were separated by a considerable interval which indicated a decided development of the pithweb and cortex. Toward the extremity of the lamina the pigmented spots were very dark and most of them were considerably elongated. They still consisted, however, for the most part, of single cells. Farther back in the transitional region, they were lighter in color, round and more

like those of the first specimen (see Fig. 3). This shows that the region of growth had been definitely localized as a meristem at the base of the lamina (as in the mature plant), while further out in the lamina growth was taking place mainly by the enlargement of cells already formed.

From this point on the development of the species was illustrated by many specimens of all ages. The first marked change was the enlargement of the primitive disc. In a specimen 30 mm. long (Fig. 15) the disc had reached a diameter of 4 mm. At this stage it bears a striking resemblance to that of the adult *Renfrewia*, being very flat and closely appressed to the substratum. As in that genus, the growth which causes the enlargement becomes localized in certain regions, giving the disc a crenate margin. In places the localization had become sufficiently pronounced to give rise to definite primary hapteres exactly as described by MacMillan ('99) for young plants of *Nereocystis* and by the writer in the adults of *Renfrewia* and *Cymathere*. These primary hapteres are of course all restricted to the primitive disc. Soon after this stage the secondary hapteres begin to arise around the base of the stipe and become very abundant, quickly obliterating the primitive holdfast. The age at which branching and differentiation of the midrib appear varies greatly. Sometimes the plant may reach a length of 80 mm., with only the beginnings of the midrib and of the splitting to form the first branch (Fig. 21); while in one plant of 160 mm. the perforation of the midrib for the branch had only just been accomplished (Fig. 22). On the other hand a specimen (Fig. 19) measuring only 18 mm. showed the position of the perforation plainly marked out. The first appearance of the midrib is indicated by two straight lines extending from the transition region up into the lamina (Fig. 20). The lamina between them grows thicker and takes on the characters of the midrib, which gradually extends toward the tip. But usually for a long time the two edges are more pronounced than any other portion of the rib.

As is well known, the whole subfamily, the *Lessoniatae*,



FIGS. 18-23. *Lessoniopsis*. Four fifths natural size.

FIG. 18. Young plant at about the same stage as Fig. 15 to which is attached another intermediate between it and that shown in Fig. 4.

FIG. 19. Plant grown in heavy surf, holdfast very large; plant dwarfed, indentation for first branch already appearing in the transition region.

FIG. 20. Plant from quiet water grown to an unusually large size, with no indication of branching, midrib just forming.

FIG. 21. Similar to the last except for the beginning of the perforation.

FIG. 22. Perforation complete.

FIG. 23. Primary branching complete, perforations formed for second branches, inner side of new laminae beginning to form from the divided midrib.

to which *Lessoniopsis* belongs, is characterized by the repeated splitting of the original unbranched lamina till the plant comes to have a cluster of many leaves. The method of this branching is peculiar to the kelps. Instead of forking at the tip or sending out a new shoot as a lateral proliferation, the branching begins in the transition region between the stipe and the lamina and extends upward until it reaches the tip of the lamina, thus splitting it, while the stipe is divided, to a greater or less extent in the different genera, by the downward extension of the same process. This method of branching is the necessary consequence of the position of the meristem, which is situated at the junction of lamina and stipe, so that all new growth is intercalated between the older portions of both. It is obvious, therefore, that any new structure, such as a branch, must originate in this region of growth.

In *Lessoniopsis* the first indication of branching appears in a slight depression in the midrib on each side of the lamina at the transition region. These depressions or pits enlarge and deepen until they meet and form a perforation almost exactly at the base of the lamina. It will be readily seen that if the split extended uniformly upward through the midrib, it would result in two unsymmetrical falcate laminae each with a rib along its inner side. This, however, is not usually the case, for new tissue forms between the divisions of the midrib and soon duplicates on the inner side the outer edge of the lamina (Fig. 24, *a*). Thus each of the new laminae is approximately symmetrical with respect to its midrib. In the stipe the branching is carried far enough to involve the whole of the meristem, so that future lengthening is almost completely confined to the stipes of the branches.

Before the new laminae have completely separated there usually begins to appear at the base of each, the second split, which is carried to its completion in the same manner as the first. Thus branching continues again and again so long as the plant lives. Since all the splitting is dichotomous, the result should be a flat fan-shaped plant,



FIGS. 24-26. Older *Lessoniopsis*. About one sixth natural size.

FIG. 24. Plant several times branched; at *a* the process of the formation of the inner side of the divided lamina from the midrib is clearly indicated.

FIG. 25. Plant with about 25 laminae, original dichotomy plainly shown.

FIG. 26. Plant still undersized but with the characters of the adult; one branch is lifted out by a background to show the sporophylls (*s*) and their relation to the ordinary laminae, which show the beginnings of division at their bases as in the younger forms.

and sometimes this form is attained even in very old plants, especially those growing in the quieter places, but usually the stipes twist more or less and spread out in all directions, giving the plant a tree-like aspect.

There is no change in this habit of growth until the plant has attained a considerable age. But long before it reaches its full size there appears another kind of lamina among the narrow ones with midribs. These lack the midribs and are much wider, with conspicuously rounded or subcordate bases. The ribbed laminae are always sterile, but these wider ones become sporophylls. Consequently after their sporangia are discharged they slough off and disappear, leaving for a time scars on the stipe. The origin of these sporophylls is evidently different from that of the ordinary laminae. Since very few new sporophylls are developed during the summer, at

least at Port Renfrew, it seems probable that their production is a seasonal phenomenon taking place only for a limited period before the fruiting season. However they are formed, they do not reach their full size at first. The youngest are always shorter and narrower than the older and entirely lack the characteristic base. Some of the smallest remind one of the young sporophylls of *Pterygophora* and have the appearance of being outgrowths from the meristem as in that species, but the writer does not feel sure that they are normal. Further information on the origin of the sporophylls will be very welcome because of its importance in determining the relationships of this plant to the other genera of kelps.

At length, by branching and production of sporophylls a plant is formed with several hundred laminae, in extreme cases reaching lengths of a meter, while the whole plant is often two meters long. The stipe at the base becomes 10-20 cm. in thickness and is marked with many annual rings of growth. The holdfast clings so tenaciously to the rocks that it will support a man's weight. On a flat bottom the plants stand upright, but they hang down when growing on an overhanging cliff, as in the photograph (Fig. 27). As in all water plants, their only way of maintaining themselves in the strong currents in which they live is by bending before them. Accordingly, rigidity is developed only in very large basal portions of the stipe, while the terminal branches have not sufficient stiffness to support the plant when out of the water. *Lessoniopsis* thrives only in places where the surf is very heavy and is there found along with *Postelsia*, the sea palm, the most typical of all the eumaphytes, but it does not withstand drying so well as that plant and consequently grows at a considerably lower level.

### C. *Egregia*

To one acquainted with the kelps only through the more widely distributed genera such as *Laminaria* and *Alaria*, *Egregia* must always be the most interesting of the family. Algologists agree in assigning to this plant the high-



FIG. 27. Lessoniopsis (hanging) and Postelsia (upright) growing on an overhanging shelf exposed to the heaviest surf. Lessoniopsis is about two meters long and Postelsia, one half meter.

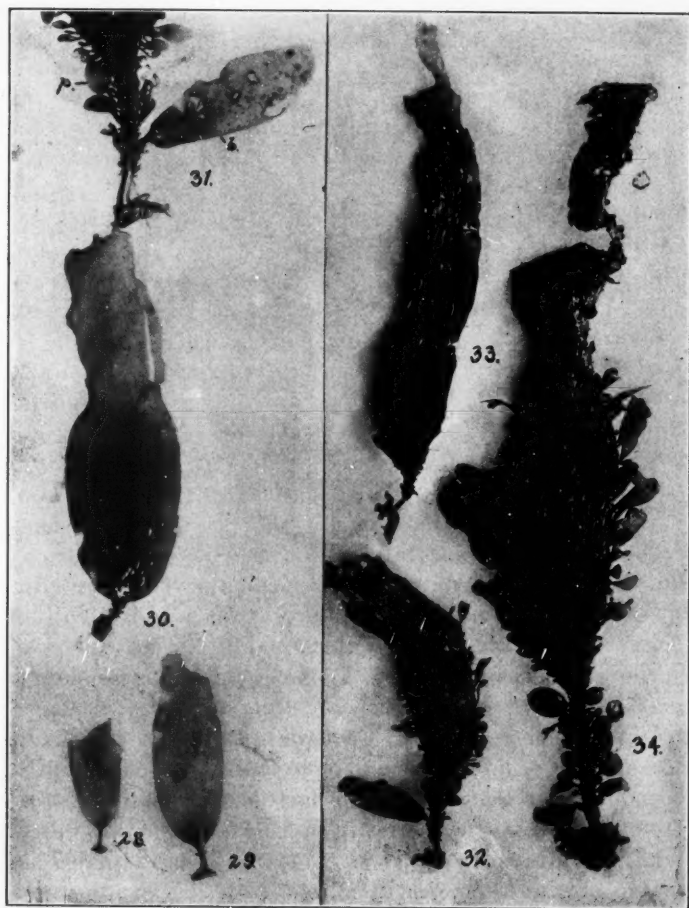
est place among the kelps as being the most specialized of them all. It is a genus of the western coast, represented by two species, one northern, the other southern. Both are extremely variable and in their many forms and intergradations present to the taxonomist a problem of more than usual difficulty. Some features of the morphology of the northern species, *Egregia menziesii*, have been presented in a paper by Ramaley ('03), illustrated with some excellent figures of adult and middle-aged plants, while Reinke ('03) has also given figures and a brief description of somewhat younger plants. The development of this species which grows abundantly at the Minnesota Seaside Station, will be worth considering in detail in connection with the other kelps discussed above because of its greater complexity.

*Egregia*, like *Nereocystis*, has an extremely long stipe; indeed, in proportion to its lamina its stipe is much longer, but its character is totally different from that of *Nereocystis*. In the latter plant the stipe stretches from the holdfast, frequently attached to a depth of twenty or

thirty feet, like an anchor rope, to the surface, where it holds the large float and laminae against the impact of the heavy surf. This stipe is often less than one centimeter in thickness for half its length, but of such surprising strength that the native fishermen tie their boats to these ready-made anchors and ride out a storm, as noted by MacMillan ('99). The stipe of *Egregia*, however, while slender and flexible, is not bare, but covered with very numerous short proliferations along its whole length giving it the appearance of a feather boa. Some of these are photosynthetic areas, some sporophylls, some floats filled with air. The presence of such organs as air vesicles so near the holdfast shows clearly the plant's adaptation to a shallow-water habitat. It grows attached to rocks which are never deeply submerged and are uncovered even by a moderately low tide, where its branches, buoyed up by their innumerable pneumatocysts, float with their whole lengths on the surface of the water. To the boatmen along that shore a thick bed of *Nereocystis* is a sure sign of deep water, but a bunch of *Egregia* as surely marks a rock to be avoided.

The youngest plants of *Egregia* are extremely difficult to separate from those of *Hedophyllum*. The juvenile forms of both these kelps are dark brown, distinguished from most others of their size by shorter stipes, together with a rather strong development of hapteres. The youngest plant of *Egregia* found (Fig. 28) was 25 mm. long, with a lamina about 20 mm. long and 10 mm. wide. The holdfast had already developed a circle of secondary hapteres, although the primitive holdfast could be made out beneath the secondary. The stipe was but 3 mm. long, cylindrical, and featureless except for a very slight thickening about a millimeter below the base of the blade. This appeared to be the beginning of the proliferations which characterize the later stages of the plant.

The thickening of the stipe soon becomes more pronounced and develops into a pair of horns about a millimeter long just below the base of the lamina and lying in the same plane (Fig. 29). These are the only dis-



FIGS. 28-31. *Egreia*. Five sixths natural size.

FIG. 28. Youngest plant, barely distinguishable from *Hedophyllum* at this age, cf. Fig. 37, which is less eroded.

FIG. 29. Plant showing the first pair of proliferations on the stipe.

FIG. 30. Plant with the transition region roughened by many capillary proliferations, tuberculate ridges appearing in the base of the lamina.

FIG. 31. Base of a much older plant showing the differentiation of the first branch (b) made evident by the appearance of proliferations on its stipe, first pneumatocyst (p) just appearing, base of stipe remaining smooth.

FIGS. 32-34. *Egreia*. One half natural size.

FIG. 32. Whole of the plant shown in Fig. 31, proliferations on the lamina absent at the tip, but well developed below.

FIG. 33. Much younger plant than Fig. 32, capillary proliferations prominent in the transition region, laminar proliferations just beginning to appear on margin of both stipe and lamina, tip of lamina smooth, other portions covered with protective ridges.

FIG. 34. Older plant in which the lamina has reached its maximum development and the stipe has begun to grow, several well-developed pneumatocysts and young branches are evident among the outgrowths from the stipe.

tinguishing features of the plant until it reaches a length of about 40 mm. In plants of about this length a few round tubercles begin to appear at the base of the lamina, which has hitherto been smooth as in *Hedophyllum*. A specimen 75 mm. long (Fig. 30) showed numerous tubercles in the transition region, giving it a roughened appearance; and there were three instead of two horns below the zone of the tubercles. The basal portion of the stipe was still smooth as in the youngest specimen. In this plant the stipe had elongated scarcely at all and the growth had been restricted to the lamina, which extended through 70 of the 75 mm. of the plant's length. Tubercles similar to those of the transition region had also appeared and these were shown by transmitted light to be connected with streaks of denser tissue running lengthwise through the lamina.

After this stage, as in *Lessoniopsis* there is some variation in the age at which the various structures appear. A specimen 18 cm. long (Fig. 33) will serve as an illustration of the next step. Here the streaks beneath the tubercles of the lamina had become prominent ridges, much larger than the small tubercles at their summits. The ridges stood out so strongly as to cause depressions on the opposite side of the lamina beneath them. This gave the lamina a wrinkled appearance and added greatly to its strength. The margin was entire or slightly undulate, but at the base were a few short serrations which looked much like the tubercles of the stipe. The roughened region of the stipe was about 1 cm. in length and no longer terete like the lower smooth portion, but somewhat flattened. In place of the horns of the younger specimens were several outgrowths, the largest of which bore a small orbicular lamina. The holdfast had become nearly 2 cm. in diameter by the great elongation of a few hapteres.

In view of the proportions assumed by the adult plant the relation between the lamina and stipe in the juvenile forms is most interesting. In the smallest specimen the lamina is only about three times as long as the stipe.

But further growth is for a time almost restricted to the lamina until the ratio is increased to ten or fifteen to one. After this stage the stipe begins to grow and soon surpasses the lamina, which seldom exceeds half a meter in length, while the stipe sometimes becomes fifteen or twenty times as long.

A specimen 12 cm. in length (Fig. 32) though only two thirds as long as the one just described, was considerably more advanced. The uppermost quarter of the lamina was entire, as in the last plant, and below the tip were a few serrations like those at the extreme base of the former. Toward the growing point these outgrowths were larger and had become spatulate proliferations about a centimeter long, fringing the basal two thirds of the blade. The stipe had reached a length of 3 cm. Its numerous tubercles were much elongated and frequently dichotomously branched, once or even twice giving the peculiar roughened appearance characteristic of the adult. The proliferations along the lateral edges of the stipe were much more numerous than in the former specimen; some of them were simple laminar appendages; others were inflated into small globular pneumatocysts (Fig. 31, *p*); on others the stalks were roughened by small tubercles like those of the main stipe. Some of these last, if detached, might easily pass for young plants cut off just above the holdfast.

Though marked changes are yet to occur before the plant becomes mature, they may be understood by a comparison of the adult with this young plant (Fig. 32). The most conspicuous change is of course the great elongation. While this is especially noticeable in the stipe, the lamina likewise grows until it reaches a length of about 50 cm., but its width increases scarcely at all, seldom exceeding 4 cm. The proliferations from this narrow lamina become so numerous that they completely mask the distinction between it and the stipe, and it is only by close inspection that the lamina may be recognized. The growth of the stipe carries the lamina far away from the holdfast, where it is exposed to the severest action of the

waves, which lash the plant until the lamina together with the meristem is torn off and there remain simply the stipe and holdfast.

The stipe remains smooth for a few centimeters above the large branching holdfast, this being evidently a persistence of the smooth basal region of the young plant. Some of the lower tubercles, however, disappear, so that the smooth area now extends farther from the base than originally. This portion is terete, but at a length of about a decimeter the stipe becomes flat and strap-like about four times as wide as thick.

In the younger specimens the proliferations from the stipe and lamina are all small and not very numerous. In the adult they enlarge very greatly and increase in numbers so as to become by far the most conspicuous feature of the plant. The increase, both in number and size, is most marked toward the growing point, those at the base generally remaining small and scattered. Farther out along the stipe they are found of all lengths up to about 12 cm. and of various forms, as figured by Ramaley. They stand as thickly as possible along the stipe; in some places by actual count upwards of a hundred were found in a single centimeter of its length. Of these only a few were large and more than half less than a centimeter long. Crowded as they are along the edges of the stipe, they never arise from its faces, which are bare except for the tubercles described above. The air vesicles are formed at frequent intervals, providing sufficient buoyancy to keep the plant floating just beneath the surface with the tips of the proliferations emerging. When mature, they are about 30 mm. long, with an average capacity of about one cubic centimeter. Others of the outgrowths remain permanently small and become sporophylls. The outgrowths on the lamina also increase in size and number, but become neither so large nor so numerous as on the stipe. As noticed by Ramaley, no bladders nor sporophylls develop on the lamina.

*Egregia* becomes much branched before it is mature. Although Ramaley suggests that the branching may have

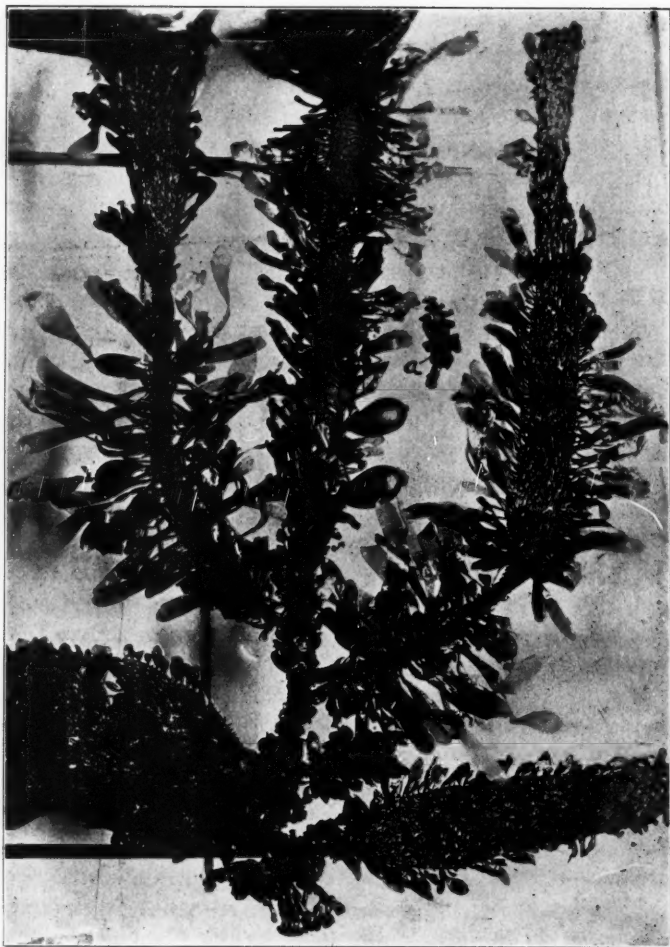


FIG. 35. *Egregia*, base of small plant with the characters of the adult except for the small number of branches, though only a few of those present could be shown, while the others were piled up in a mass to the left of the holdfast, (a) a dwarfed branch with a frilled margin. One fourth natural size.

an appearance similar to *Lessonia*, it is brought about by a fundamentally different process, as has already been noted by Setchell ('93) and by Reinke ('03), who figure several stages in the development of a branch. Some of the earlier proliferations, as stated above, soon develop roughenings on their stalks like those of the main stipe and take on the appearance of younger specimens of the species (Fig. 31, *b*). This is the first external indication of an important difference in the constitution of these outgrowths from the ordinary proliferations. For in them has become differentiated a meristem independent of that of the primary branch. They develop exactly as did the main axis and soon become indistinguishable from it except in the manner of attachment to the holdfast, possessing all the structures which have been described for a primary branch including other branches which in turn go through the same process. After several such branches have been formed there is a modification of the process. The laminae are dwarfed, while their margins become conspicuously puckered and ruffled (Fig. 35, *a*). Sometimes the ruffles are so pronounced as to completely enfold the meristem. In such a branch proliferations from the lamina appear very late, but the ruffle gives it a similar aspect. The dwarfed condition of the laminae persists until the stipes become several centimeters in length, when the usual relations of stipe and lamina become manifest. Though roughening may appear on other parts of the plant, the development of meristematic proliferations is confined to the basal portion; branches do not develop at a distance much exceeding 20 cm. from the holdfast. Around the base of any old plant there is always a large number of short branches in all stages of development, but there are not often more than a dozen long branches at any one time. The general appearance of the numerous dwarf branches suggests that they may not have a rapid development like the first branches, but rather grow very slowly or lie dormant for a time like the dormant buds of trees.

This method of branching is peculiar to *Egregia* and, as



FIG. 36. *Egregia* growing in a thick bed of kelp in which are prominent *Alaria* (with a midrib) and *Hedophyllum* (in foreground, especially at right).

far as the writer knows, nothing like it occurs in other kelps save in *Thallasiophyllum*. It is a matter of great interest from several points of view. Morphologically it gives the best reason for considering *Egregia* the highest of the *Alariata*, although that position would probably be accorded it without question because of the differentiation of the ordinary proliferations alone. The other members of this subfamily produce outgrowths which function as sporophylls, and in some of them, *e. g.*, *Eisenia*, these become the main photosynthetic areas of the plant. The development of meristems in such outgrowths, leading to the formation of branches, is the next step towards greater complexity and the logical summit of the *Alaria* series. But its greatest interest is from the ecological point of view. The extreme length of the stipe pushes the growing point far out, where it is lashed severely by the waves and frequently destroyed. Were the plant dependent on this for its continued healthy existence, as in *Laminaria*, it might easily be killed or at least handicapped for a considerable part of the time by the loss of the blade until a new one could be regenerated, as in many species of *Laminaria*. But, should the older branches be injured, these basal branches may develop at any time. By their

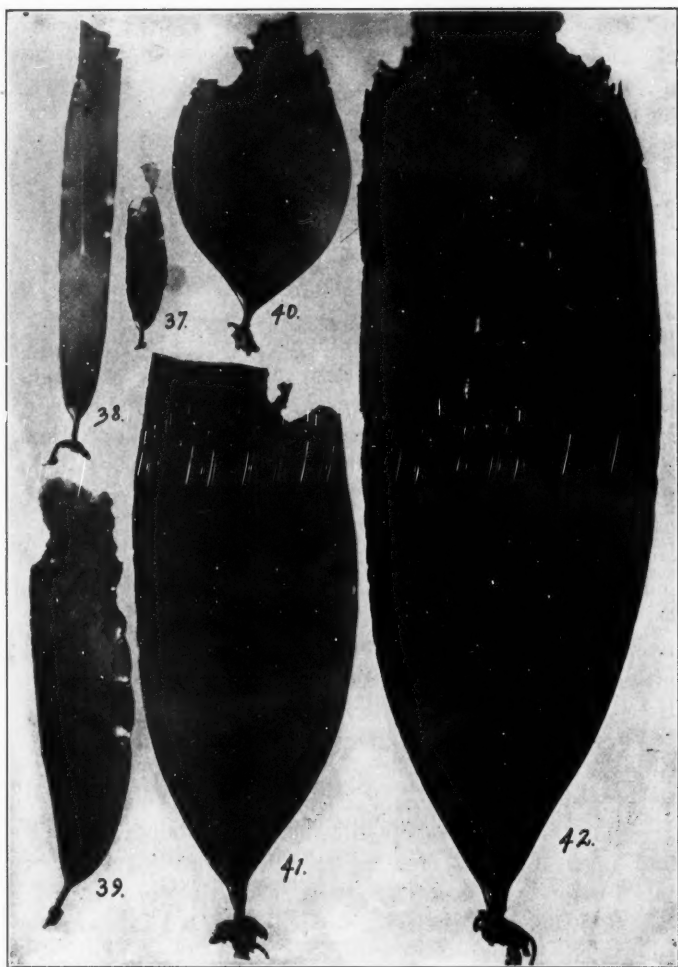
presence the plant is practically possessed of a new basal meristem supplementing and to a certain extent supplanting the primary meristem. Once established in a favorable situation, a plant may therefore maintain itself indefinitely, casting off old branches and developing new ones continuously.

#### D. *Hedophyllum*

Because of the close similarity of the young stages of *Egregia* and *Hedophyllum sessile* it will be of interest to add a short description of the latter. It has already been the subject of considerable study by Setchell, who has published ('05) a discussion of its development well illustrated by figures. His paper, however, was written from another point of view than the present, namely, the relationships of *Hedophyllum sessile* to the other species of *Hedophyllum* and to *Agarum* and *Thalassiohyllum*. Since from this standpoint the very young forms of *Hedophyllum* are not important, Setchell was not particular to obtain plants less than about 5 cm. in length. But for a comparison with *Egregia* the younger forms are of the most interest. This species<sup>2</sup> is extremely abundant at the Minnesota Seaside Station, outnumbering in individuals any other kelp present on that coast. It grows at the highest level occupied by the kelps, and in various situations as regards wave action.

Very young plants of *Hedophyllum* are difficult to distinguish with any certainty from *Egregia* and from the various species of *Laminaria* growing in the same locality. *Hedophyllum* is, however, much more abundant in adults and juvenile forms, and as the specimens selected were taken from beds composed mostly of *Hedophyllum*, the probabilities are greatly in favor of a correct determination. The youngest plant (Fig. 5) measured approxi-

<sup>2</sup> Though Puget Sound is given as the southern limit of the other American species, *Hedophyllum subsessile*, I have been unable to satisfy myself of its occurrence at Port Renfrew. Two distinct series of juvenile forms are, however, represented there, one with a narrow blade like those which Setchell figures, and, as here described, another with a very broad, cordate blade even when very young. What the relations of these may be to the adult plant I have not yet fully determined.



FIGS. 37-42. *Hedophyllum*, series of young plants showing the gradual obliteration of the stipe by the broadening of the transition region, and the origin of new hapteres higher and higher up the stipe. Four fifths natural size.

mately 2.3 mm. in length and the margin of the primitive disc was nearly smooth. The edge of the lamina was only one cell in thickness, but there were evidently several layers in the middle region and toward the base. In a specimen 6.5 mm. long the holdfast had become distinctly crenate around the edges and the one-layered lamina had disappeared. The crenations had become much more pronounced and had assumed the characters of primary hapteres in a specimen 10 mm. long (Fig. 6).

By the time the plant reaches the length of an inch its determination is not difficult. A specimen 28 mm. long (Fig. 37) will serve for comparison with the youngest *Egregia* described. The lamina is narrower and longer than in that plant; the holdfast has not as yet developed secondary hapteres and the stipe is shorter. Though the stipe always remains short, it usually becomes longer than is shown in this plant (about 5 mm.). The narrowness of the lamina is characteristic, but is not sufficiently marked at stages earlier than this to render diagnosis easy.

Soon after this stage secondary hapteres begin to appear above the primitive holdfast. Though they arise in circles as in the other kelps, they usually develop quite unevenly in the young plant, some members of the circle becoming long, while others are yet mere knots on the stipe. When a length of about 8 cm. is reached the stipe begins to thicken and flatten. The transition region, which has been sharply marked off, becomes less and less distinct and the plant comes to consist of a lamina with a cuneate base anchored by the holdfast (Fig. 42). This condition sometimes persists until the plant has reached a considerable size. More usually, however, the broadening continues and quickly brings about the adult condition.

When mature (Fig. 43), *Hedophyllum sessile* becomes a broad, cordate, sessile plant anchored by a mass of hapteres at its base. Its lamina is torn to ribbons like a digitate *Laminaria*, so that it may resemble one of the kelps with true branching. The hapteres arise in circles one above the other higher and higher up on the stipe

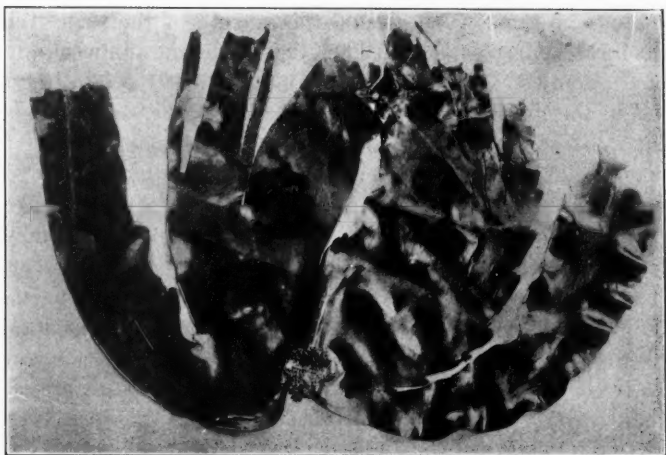


FIG. 43. *Hedophyllum*, medium-sized plant showing the cordate lamina torn by the waves. A fully mature specimen would be a rosette so dense that its structural relations could not be made out. One fifth natural size.

until they obliterate it and even come to grow out from the lamina itself. Thus there arises a thickened basal portion of the lamina which forms a conical holdfast, as in the other kelps, while new circles of hapteres may be seen on its upper edge, growing out from the undifferentiated lamina. By this process the holdfast region extends beyond the bases of the segments of the lamina so as to give the old plant the appearance, not of one, but of several independent laminae springing from a common holdfast. Considering the similarity of the young plants to *Egregia*, the divergence of the adults is very striking.

(To be concluded)

## THE LARVA AND SPAT OF THE CANADIAN OYSTER

J. STAFFORD, M.A., PH.D.

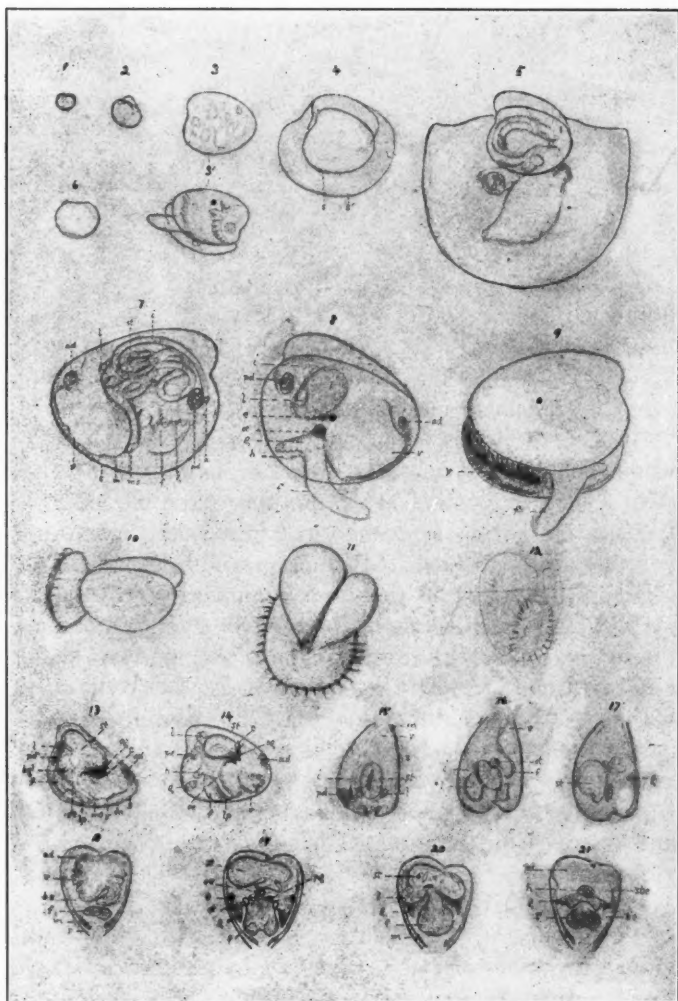
MONTREAL

### I. THE LARVA

IN the summer of 1904, at Malpeque, Prince Edward Island, on behalf of the Canadian Marine Biological Station, I undertook to gather what information I could upon the life of the oyster from the time it becomes a distinct bivalve veliger to the time when it is recognizable by every oyster fisherman as a spat oyster.

Brooks, of Johns Hopkins University, Baltimore, to whom belongs the immortal glory of having discovered that American oysters are unisexual and that artificial fertilization of the eggs and rearing of the larvæ are possible, had worked out the spawning, fertilization, segmentation, gastrulation and organization up to the earliest microscopic free-swimming bivalve veliger, and there was no lack of literature on oyster culture beginning with macroscopic oyster spat of, let us say, the size of one's thumb-nail. But the intermediate stages, mostly microscopic, seemed to be scarcely, if at all, known, and there were many questions as to the time and place where they might be found as well as to their anatomy and comparison with other genera which required investigation.

The possibility of raising young oysters from eggs and keeping them alive without admixture with other individuals or other species until one had seen the whole series of continuous transformations into the adult seemed next to impossible. I chose rather to learn to recognize the larval oyster in plankton collections, a method which had apparently received no attention. I



## EXPLANATION OF PLATE

*a*, anus; *ad*, anterior adductor muscle; *bc*, branchial chamber; *bgl*, byssus gland; *c*, chitin; *e*, eye spot; *f*, foot; *g*, gills; *h*, heel of foot; *i*, intestine; *l*, liver; *lp*, lower lip; *m*, mantle; *mo*, mouth; *oe*, oesophagus; *og*, supra-oesophageal ganglion; *ot*, otocyst; *pd*, posterior adductor muscle; *pg*, pedal ganglion; *s*, larval shell (prodissocoenoch); *s'*, spat shell (dissocoenoch, neplonic); *sdc*, supra-branchial chamber; *st*, stomach; *v*, velum.

FIGS. 1, 2, 3, 4, 5. Development of Canadian oyster from bivalve veliger to young spat. From the right side, drawn under the same conditions throughout, Leitz microscope, oc. 3, obj. 2 (revolver). Zeiss Zeichenapparat. Drawing desk flush with stage and slanting upwards at proper angle to prevent distortion.

Measured under Leitz oc. 5 and obj. 4 with a Leitz oc. microm. valued by a Leitz stage microm.

FIG. 1. Oyster larva, young straight hinge stage. .089 mm. high, .103 mm. long.

" 2. Oyster larva, early umbo stage. .138 x .144 mm.

" 3. Oyster larva, full grown. .31 x .34 mm. Fig. 3' from the left side.

" 4. Oyster spat, with the valves of the larval shell (prodissocoenoch) plainly retained. .51 x .55 mm.

" 5. Oyster spat. .876 x 1.030 mm. The larval shell is .369 x .384 mm.

" 6. Same as Fig. 1 drawn under oc. 3, obj. 4, for comparison with Figs. 7, 8, 9.

FIGS. 7, 8, 9. Same as Fig. 3 drawn under oc. 3, obj. 4.

FIG. 7. Oyster larva from the left, with several organs sketched in.

" 8. Same from the right, with dorsal hinge-line tilted towards the observer.

" 9. Same from the left, with ventral gaping margin tilted towards the observer.

FIGS. 10, 11, 12. Free-hand drawings of full-grown living oyster larvae, not so highly magnified as Figs. 7, 8, 9.

FIG. 10. Oyster larva, full-grown, from the left, velum protruded and partly expanded.

" 11. Same from behind, attached to the slide by its fully expanded velum, large left valve.

" 12. Same from the ventral surface, velum partly protruded.

FIGS. 13, 14, 15, 16, 17, 18, 19, 20, 21. Sections of full-grown larvae, drawn free-hand.

FIG. 13. Section median sagittal (nearly), from the right. The foot being turned sideways was not split medially.

" 14. Same of another series.

" 15. Section horizontal (upper), from above.

" 16. Same (deeper).

" 17. Same (lower).

" 18. Section frontal, transverse (anterior), from behind.

" 19. Same (median).

" 20. Same (near middle) of another series.

" 21. Same (posterior) of same series as 18 and 19.

had never seen an oyster larva or a young spat, but I had followed the main stages in the life history of the mussel.

Beginning my plankton-collecting at the end of the first week in July, it soon became apparent that there were many species of bivalve larvæ present in the water, and in order to refer these with some precision to the proper adults it would be necessary to carry on at the same time a faunistic study of the Mollusca of Richmond Bay. The commonest of these relative to my purpose were found to be species of *Mytilus*, *Mya*, *Venus*, *Clidiphora*, *Ostrea*, *Anomia*, *Mactra*, *Modiola*, *Pecten*, *Saxicava*, *Macoma*, *Ensis*, *Yoldia*, etc., and to find larvæ corresponding to all of them was beyond my ability. Nevertheless, several larval forms gradually became familiar and I referred them provisionally to certain adults. On the twenty-fifth of July what I took for oyster larvæ (Plate, Fig. 3) first decidedly claimed my attention and as time went on I became more and more convinced of the correctness of my surmises. But belief is not proof, so I set to work experiments with a view to entrap oyster larvæ on glass plates at a time when presumably the larvæ become too heavy to swim with ease, settle towards the bottom, creep about and select some clear, solid surface upon which they fix themselves and transform into the youngest oyster spat. This was successfully accomplished on the sixteenth of August when I obtained a minute oyster spat (Fig. 5) still preserving most evident characteristics of the larva, but with the addition of a rim of spat-shell, and later I found many minute spat-oysters on various natural objects such as shells and stones.

The plankton was collected in conical nets, made of fine-meshed silk bolting cloth, attached at the broad end by a rim of linen to an iron ring one foot in diameter, to which were tied, at equal distances, three pieces of cod-line, the other ends being brought together and secured to a towing line. The small end of the net was also

furnished with a linen rim in which was tied the neck of a wide-mouthed bottle. To the towing line, in front of the net, was fastened a sinker and the whole was dragged through the sea-water, behind the little steamer *Ostrea*, under reduced speed, for about a mile, when the net was hauled up, the contained water carefully drained through one side, after which it was dipped several times right side up into the sea and raised so as to wash all the plankton material down into the bottle. The bottle could then be removed and corked, the net washed by throwing it overboard again open, and other bottles used for different places or different depths on the same excursion.

In such a manner may be procured a wealth of plankton material, but slight modifications in mode of operation may be employed, depending upon the nature and object of one's research. The older bivalve larvæ are compact, heavy, well protected, so that they will stand comparatively rough usage. By the time one reaches the laboratory the great mass of the copepods may be dead and sunk towards the bottom of the bottle, but underneath this mass one can see the darker, granular, more sand-like bivalves. These may be withdrawn by a glass tube and emptied into a watch glass, the more superficial, lighter things being again removed by a pipette. In this way bivalve larvæ may be obtained, sometimes by thousands, and almost entirely free from admixture with other animals, while among them, if collected at the proper time and place, will occur oyster larvæ.

At Malpeque the full-grown, free-swimming, pelagic, or more or less abyssal, or creeping larva of the oyster (Figs. 3, 7, 8, 9) possesses a characteristic brownish-red color—suggestive of the soil of its native island shores—a shade which enables it to be immediately distinguishable from every other bivalve larva with which it is associated. The shell (prodissoconch) is asymmetrical, inequivalve and inequipartite, the left valve being larger, more convex and with a large umbo, the right one smaller, flatter

and with a moderate umbo, while the umbos have a postero-dorsal position, projecting backwards and upwards and making the shell broader, deeper, squarer behind and tapering but rounded in front. The largest measure about .358 by .365 mm. in height and length, but, owing to the different convexities of the valves, the greater breadth above and behind, and the different degrees to which it may be tilted in this way or that, the same larva may vary much in apparent size and shape according as to how it is presented to the observer. The following are measurements of half a dozen larvæ at different ages selected from a large number of records: .131 x .138 mm., .138 x .144 mm., .207 x .241 mm., .241 x .276 mm., .296 x .345 mm., .345 x .372 mm. The larval shell of the young spat (Fig. 5) measures .369 x .384 mm. and may be taken to represent the maximum size.

When mounted on a slide the larvæ are accustomed to remain quiescent, and from their deep coloration are difficult to examine, but sometimes a more transparent one permits certain organs to be traced. When freshly collected and examined in a watch-glass of pure, cool water from their native habitat, many of them exhibit the greatest activity, swimming hither and thither or circling round and round by means of the velum (Figs. 9, 10, 11, 12), a swimming organ which they protrude between the antero-ventral margins of the shell-valves and expand in a manner resembling the opening of an umbrella. The margin of this is densely covered with large cilia, the violent flapping of which propels the animal forwards with the heavy body and shell suspended beneath the velum. Jarring the watch-glass will cause the animal to immediately withdraw its velum (Figs. 7, 8), at the same time snapping the valves of its shell together and dropping towards the bottom. Such observations illustrate the ordinary mode of locomotion and the response to violent movements in the sea, for during heavy gales a plankton net will take few or no larvæ near the surface.

An organ of immense interest to zoologists and of vast

importance to the animal is the foot (Figs. 7, 8, 9), a structure which I claim the privilege of having first recognized. The adult oyster is normally a quiescent, sessile animal, having its left valve solidly cemented to a rock or another shell. Under these conditions a creeping foot, such as is possessed by a clam, a mussel, or a quohog, would be of no service to the oyster, which in fact has none. Influenced, no doubt, by this difference in the adults, zoologists have been accustomed to think of the oyster larva as being vastly different from other bivalve larvæ, and repeatedly state that it has no foot, a misconception which justifies the view with which I started out, viz., that plankton stages of oyster larvæ have been neglected, embryologists jumping from early veliger or phylembryo to late prodissoconch or early nepionic periods. The foot, at the period we are studying, is well developed, and is a most capable organ, by means of which the animal can creep rapidly about and forcibly flop its heavy shell from one side to the other. When extended it is a long, slim, ciliated, muscular outgrowth from the middle of the ventral surface of the body of the larva, behind the velum. Its lower or posterior surface sometimes appears flattened or even grooved lengthwise (Figs. 18, 19, 21), and at a short distance from the base of attachment there is a heel-like projection (Figs. 8, 9, 13, 14, 21) which doubtless contains the opening of the byssus gland. When quiescent the foot is shortened, retracted and closely tucked away behind the velum and between the gills, but it can stretch so far as to perform feeling movements over all parts of the body within the shell and even bend up along the outside of the shell. I have no doubt that at the end of the free-swimming period, when the velum fails as an organ of locomotion and the larva has to remain at the bottom, the foot then proves to be of greatest service in freeing the little animal from overwhelming sediment, creeping on to a solid substratum, clearing a suitable place for fixation, and perhaps furnishing a transitory byssus.

Lying against the inner sides of the shell-valves are right and left folds of the mantle (Figs. 7, 18, etc.), the free edges of which secrete the shell material and may, like velum and foot, at times protrude beyond the margin.

Along each side underneath the mantle, past the base of attachment of the foot to the body, lie the gills (Figs. 7, 8, 9, 19, 20, 21), extending backwards and downwards to near the posterior edge of the shell; in the oldest free-swimming larva there are about eight filaments in each series, diminishing in size from before backwards, the last ones being mere knobs; their lower ends are free, but their upper ends spring from one continuous fold that, behind the foot, joins its mate of the opposite side, near the margins of the mantle. They correspond to the right and left inner gills of the adult oyster.

The alimentary canal (Fig. 7) is much longer than the body and in consequence has become folded, the greater part lying to the left (Figs. 17, 19, 20) of the median sagittal plane, but mouth, œsophagus and anus are median. The mouth (Figs. 7, 13) is a funnel-shaped opening lying immediately below and behind the velum, to which its walls are attached and with which it is protruded and withdrawn, so that it can only be functional while the velum is to some extent expanded, when the activity of its cilia may also contribute to the process of feeding. The œsophagus (Figs. 7, 13, 14, 19) lies between velum and foot in the median sagittal plane as well as in or very near the median transverse plane of the body. Here it passes dorsalwards, between the first gill-filaments, and opens into the stomach with its large brown lateral liver-sacs. The intestine passes backwards towards the right and then forwards towards the left, when it again turns backwards and upwards in the left umbo and finally downwards in the median plane over the posterior adductor muscle.

In front and above the velum is an anterior adductor-muscle (Figs. 7, 13, 18, etc.), running transversely between the valves, while below the posterior parts of the

umbo is a larger, transverse posterior adductor muscle (Figs. 7, 13, 21, etc.). Retractor fibers converge from the velum to points in the umbos and there are intrinsic muscle fibers in the velum, the foot and the mantle.

About the center of the animal, as viewed from one side, and anterior to the gills are two conspicuous, black pigment spots (eye specks, Figs. 3, 8, 9, 19) that, in transverse sections of the larvæ, are found to be situated right and left on the lateral walls of the body, just in front of where their ectoderm becomes continuous on to the outer surface of the first gill filament.

Immediately behind and below the pigment spots, but on a deeper level, are right and left otocysts (Figs. 8, 9, 16, 19), each containing about a dozen otoconia. Sections show them to be placed laterally in the proximal part of the foot, close to where its ectoderm passes over on to the inner surfaces of the first gill-filaments. Between the otocysts, and of course behind the œsophagus, are the two connected pedal-ganglia (Fig. 19), and at the center of the base of the velum, in front of where the œsophagus joins the stomach, is the supra-œsophageal ganglionic mass (Figs. 13, 14), protected in front by what appears to be a yellowish-brown, flexible, chitinous layer which gives origin to the muscle-fibers of the velum.

Transverse, sagittal, and horizontal sections (Figs. 13-21) of oyster larvæ, prepared in the usual way by decalcifying the shells, staining in alum-cochineal, embedding in paraffin, sectioning with a Yung microtome, and mounting on a slide in Canada balsam, have contributed much towards an accurate understanding of the relative positions of the organs.

Development naturally begins with small, simple eggs and proceeds to larger and more complex larvæ. By the time I had become oriented with regard to the latter and proved to myself that they can actually metamorphose into oyster spat it was of course too late for that season to obtain and follow the growth of the youngest larvæ. Examination of preserved plankton collections, however,

although far from being as satisfactory as fresh, living material, shows oyster larvæ (Figs. 1, 6) but little older than the stages at which the observations of Brooks closed, viz., six days old from the date of fertilization. Brooks did not give measurements, so that it is impossible to be exact on this point—I can only judge from the shape and organization. Plankton collected July 11, 1904, between Curtain Island and Ram Island contains an abundance of minute, transparent bivalve larvæ (phylembryos) in what may be known as the straight-hinge stage to distinguish them from the older larvæ with high umbos (the umbo stage) that obscure and modify the hinge line. A hasty and superficial observation of these combined with the fact of their occurrence in proximity to oyster beds might easily lead to the conclusion that they are all oyster larvæ. But they are not. Many of them are clams, a few are mussels, and one in a great number is an oyster. A full statement of how I have determined this would require too great a digression and will be dealt with in another paper, but it results from a comparative study of bivalve larvæ in the different localities of the Biological Station combined with researches into the distribution of adult forms. Adults of the above-mentioned genera are easily distinguished; the full-grown larvæ less easily, for, since they bear little resemblance to the corresponding adults, other marks of distinction have to be selected; but the young larvæ are still more difficult, for, according to the biogenetic law, the younger they are the more nearly they resemble some stage of the common original ancestor and of course approach one another in likeness. Under such conditions the practicable, distinguishable characters may again be different and require a more critical scrutiny. Since I first turned my attention to bivalve larvæ I have found it necessary to change my point of view and mode of procedure. One can not safely trust to the eye in judging proportions, but must resort to a definite and unvarying method of measuring by means of ocular and stage micrometers.

For each of the commonest species a table of lengths was prepared, jumping only one of the smallest units of my ocular micrometer at a time, and the heights were filled in as individuals of these lengths occurred. Thus larvæ of the mussel, the clam and the oyster, at the period we are considering, measure as follows:

	Length.	Height.	Length of hinge-line.
Mussel .....	15	10	11
Clam .....	15	13	10
Oyster .....	15	13	7

—a table which will immediately make apparent the truth of many of my statements. The eye can easily perceive a difference in the proportions of the mussel and the clam, but it requires a certain refinement of judgment to do the same for a clam and an oyster. Such an oyster larva actually measures .103 x .089 mm. in length and height, and has a short, slightly concave hinge-line of scarcely half the length of the shell.

I have said that in collections of straight-hinge larvæ but one in a great many is an oyster. A similar statement might be made for any period in the larval existence of the oyster. Upon one occasion when the umbo-stage was most abundant I estimated that there was only one oyster among twenty-five bivalve larvæ. Another time I found that when the plankton net was towed at the surface against a wind it caught about a quarter as many oysters as in going back over the same distance with the net sunk a few feet below the surface of the water.

I am of opinion that the study of plankton collections for bivalve larvæ will be found a most useful help in determining the breeding season—that is to say the height of the breeding season. From the foregoing pages it may be concluded that oyster larvæ are present in the water from the eleventh of July to the first September, and that oyster spat are present from the sixteenth of August. This would seem to indicate that the second half of August is taken up with the last stages of growth of late larvæ and that the period of growth of the masses

falls between July eleventh and August sixteenth. Taking it that the youngest larvæ I have described are little older than those of similar shape and structure described by Brooks, and allowing a possible retardation on account of the climate, we should conclude that the eggs were deposited pretty close to the first of July. That spawning does not take place much before this I judge from the fact that in 1905, while I was at Malpeque preparing the station for removal, I took plankton at intervals between June seventh and twenty-sixth and this shows no oysters and but few mussels and clams.

In the microscopic examination of the genital organs for the purpose of determining the time of sexual maturity, unless one examines a very great number taken from many different localities, he may light upon an abnormal number of individuals that are immature or that have already spawned and so form a wrong conception as to the period of maximum spawning. Combination of both methods should give the best possible results.

I have purposely attempted to disregard the statements of others in order to be entirely unbiased as to my results, and from the facts of my own observations I am disposed to think that the period of maximum spawning falls in July, but that a few may spawn earlier and a greater number may straggle in later.

It is a matter of regret to me that it did not fall to my lot to begin the study of oyster larvæ during the first summer at Malpeque, for then I could have used the second summer to verify, fill in details, and follow out suggestions. I have looked forward ever since for an opportunity to do so, and this is my chief excuse for the delay in publishing these results.

Chief points of importance resulting from the foregoing work are:

1. Larval oysters are present suspended in the water of Richmond Bay, Prince Edward Island, in July and August.
- .

2. They may be taken in a plankton net at the surface and at various depths.

3. All stages from the freshly fertilized egg to the full-grown larva must be there.

4. The free-swimming period is, perhaps, considerable, close on a month.

5. They feed and grow, while in the free-swimming state, through a straight-hinge to an umbo-stage.

6. Normal fixation takes place when the larval shell is about .38 m. in length, and then the spat period begins.

7. A metamorphosis occurs through loss of larval organs as velum, foot, eye-spot, otocysts, etc., and a development of new organs as spat-shell, additional gills, palps, etc., is begun.

8. The larval shell is asymmetrical, as is also to some extent the contained body.

9. A foot, homologous with that of mollusks in general, is present in the older larvæ.

10. The otocysts contain otoconia.

11. Pedal ganglia are present.

12. A byssus-gland is present.

13. Gills are present.

14. Eye-spots are present.

15. A rigid system of measurements has been used, and a comparison of actual sizes at different periods of growth introduced.

16. Numerous niceties of structure, shape, color, activity, time, place, etc., are noted.

17. The spawning period has been limited.

18. Attention is directed to the importance of these theses and observations as bearing upon problems and methods of oyster culture.

#### LITERATURE

European works referring to the development of the oyster larva are those of:

1. 1854. Lacaze-Duthiers. Mém. sur le dévelop. des Acéphales Lamellibr. *Comptes Rendus heb. des Séances de l'Acad. des Sciences*, Paris, XXXIX, pp. 102-106. Nouvelles observ. sur le dévelop. des huîtres. Same vol., pp. 1197-1200.
2. 1882 ('83). Horst. A Contrib. to our Knowl. of the Develop. of the

Oyster (*Ostrea edulis* L.). Bull. U. S. Fish Com., II, pp. 159-167, 12 figs.

3. 1884 ('86). Horst. The Develop. of the Oyster (*Ostrea edulis* L.). Rep. U. S. Fish Com., pp. 891-910, Pls. I and II.
4. 1883. Huxley. Oysters and the Oyster Question. *Eng. Illus. Mag.*, Oct. and Nov., pp. 47-55, 112-121.

American work must be considered to have originated with Brooks, whose discoveries inspired investigators at home and abroad and pointed the way to possibilities and methods of culture that were ably carried forward by Ryder, Winslow, Rice and others. Of the many papers, reprints, summaries, etc., published by Brooks I mention but one:

5. 1880. Brooks. Development of the American Oyster. Rep. of the Com. of Fish. of Maryland, pp. 1-18, 10 pls.
6. 1882 ('83). Ryder. On the Mode of Fixation of the Fry of the Oyster. Bull. U. S. Fish Com., II, pp. 383-387, 9 figs.
7. 1882-83 ('84). Ryder. A Sketch of the Life-history of the Oyster. 4th Ann. Rep. of the U. S. Geol. Surv., pp. 317-333, pls. 73-82.
8. 1882 ('84). Ryder. The Metamorphosis and Post-larval Stages of Development of the Oyster. Rep. U. S. Fish Com., X, pp. 779-791.
9. 1884. Ryder. A Contrib. to the Life-history of the Oyster. Fisheries and Fishery Industries of the U. S., Sec. I, pp. 711-758.
10. 1882 ('84). Winslow. Rep. of Exper. in the Artif. Prop. of Oysters. Rep. U. S. Fish Com., X, pp. 741-762.
11. 1889. Jackson. The Develop. of the Oyster with Remarks on Allied Genera. *Proc. Bos. Soc. Nat. Hist.*, XXIII, pp. 531-556, 4 pls.
12. 1890. Jackson. Phylogeny of the Pelecypoda. *Mem. Bos. Soc. Nat. Hist.*, IV, pp. 277-400.

Canada has done little towards a scientific study of oyster development. Three rather unpretentious articles are known to me.

13. 1895 ('96). Prince. Peculiarities in the Breeding of Oysters. Special Reports, Ottawa, pp. 10-13.
14. 1904. McBride. The Canadian Oyster. *The Canadian Record of Science, Montreal*, IX, July, pp. 145-156, Figs. 1-4.
15. 1905. Stafford. On the Larva and Spat of the Canadian Oyster. *THE AMERICAN NATURALIST*, Boston, pp. 41-44. (Preliminary to this paper.)

#### BRIEF NOTES AND CRITICISMS

Brooks (No. 5, p. 25, of the preceding list) says: "All my attempts to get later stages than these failed, etc." He refers to his Figs. 44 and 45 which were perhaps a little younger than my Fig. 1 and were six days old. I never could understand the claim that they might develop to this stage in twenty-four hours.

Horst (2, 165; 3, 904) was unable to get stages older than his Fig. 12, a straight-hinge shell of .16 mm., which according to Ryder (7, 791) would be equivalent to an American larva of half this length, *i. e.*, little younger than my Fig. 1. He adds: "I have also been disappointed in my attempts

to procure oysters in these phases of development by means of catching larvæ floating about in the sea."

Ryder's papers (6, 383; 7, 328-9; 9, 727) are not easy to correlate on account of discrepancies in measurements or magnifications, age and occurrence, a misuse of the term embryo, etc. Making allowance for these, and combining his statements in the probable order in which they were written, I conclude that Ryder had seen two stages approximately of the same age as two I have figured. His Fig. 1, magnified 183 times measures 14.5 mm., which would give the larva an actual length of .08 mm. His Fig. 3, magnified 96 times, measures 29 mm. and similarly gives the young spat an actual length of .3 mm. But his were both fixed, and in fact it was this property which in Ryder's methods afforded the chance of their being observed. He appears to have believed that the larger one (C.  $\frac{1}{80}$  in.) marked the proper stage of fixation but that under "favorable circumstances" larvæ of the size of the smaller might become fixed and then grow to the size, shape and structure of the larger, at which time they first become spat. Considering that he obtained the small ones but once, that they were attached in no regular position, and that the one figured was on its right side instead of on its left, it seems more probable that the fixation was of a transitory nature (as regarded by Jackson) or that it was abnormal, due to unfavorable artificial conditions and that the normal process is for the larva to remain free until it reaches the size of the prodissoconch in the umbo of the young spat shell. Ryder's view of the duration of the free-swimming period as limited to twenty-four hours comes nearer to a possibility if we remember that he doubtless had in mind this case of abnormally early fixation. A similar statement might be made with regard to the sentence "The difference in magnitude between the oldest artificially incubated fry seen by me and that of the youngest fixed embryos which I collected is very small." These also agree very well with the larvæ raised by Brooks and by Horst. He never saw larvæ between these two stages in size. This represents a period during which the larvæ had to grow to nearly four times their former diameter and undergo a very great increase of organization. If the smaller stage can be raised as in Brooks's larvæ in six days the larger might require four times six days additional, making a month for the complete larval development. This time according to Brooks, Ryder and others might be reduced by very warm weather. It is just possible that too high a temperature of small isolated quantities of water may be one of the adverse conditions which have prevented larvæ from being raised beyond this stage. In nature they not only have a broader source of food supply but they can also sink into cooler water.

Winslow (10, 757) thought that the oyster larva is predisposed to fix itself very soon after segmentation and when the shell is developed to a slight extent the larvæ remain quiet in one place at the bottom. I can believe that they do not by their own efforts travel very far from the place of their origin for their locomotion is largely a circling or to-and-fro movement, but while suspended in the water they may be transported by tidal currents.

Jackson (12, 300) wrote: "Between the stage Fig. 25 and our next stage, Pl. XXIV, Figs. 1, 2, there is a blank in the knowledge of the

development of the oyster. It has not been described in the European species, and all attempts to obtain it in our own species have failed. In artificial confinement the oyster dies at this stage." His Fig. 25 is Huxley's cut of a straight-hinge larva. Figs. 1, 2 of Pl. XXIV are Jackson's own youngest stage of the spat, obtained August 4, 1888, on glass put in a drain-pipe trap on a sand-bar in Buzzard's Bay. It was firmly attached by the ventral margin of the left valve and as it had been attached less than twenty-four hours the anatomy and shell must have been developed while it was a free larva. The figures measured 37 mm. and as they are magnified 120 diameters the actual length of the recently free larva, now a fixed spat, was nearly .31 mm.

Prince (13, 13) makes the statement: "I captured many small embryo-oysters several miles from any known oyster areas," but as no measurements or drawings accompany the paper one can not judge of their size or age.

McBride (14, 151, 153) says: "Judging from the size of free-swimming larvæ caught by the tow-net . . . During the latter part of the month (August) the waters were swarming with larvæ which, from their exact agreement in shape and appearance with the larvæ of the European oyster, were doubtless the later stages of the free-swimming young of the Malpeque oyster. . . . The later larvæ which were captured by the tow-net are characterized by possessing a straight hinge to the shell. . . . Fig. 4. Late Larva of the Oyster captured by the Surface-net." The so-called late larvæ are in the light of my researches in reality somewhat early larvæ. Late larvæ would be more appropriately applied to the umbo-stage which doubtless was in the water at the time referred to, but was at that time unknown as a plankton organism. The statement that the waters during the latter part of August were swarming with young straight-hinge oyster-larvæ does not correspond with what I found at the same place the succeeding year. Upon examining Fig. 4 I find that it is not an oyster larva. The measurements are 83, 70, 51 mm. which if divided through by 5.53 will give 15, 12.6, 9.2 mm. as the length, height and hinge-line. Referring this to the table of comparison of a mussel, a clam and an oyster at this period, on a former page, it becomes evident that it could have been no other than the larva of the clam.

The shell of the larva was held to be perfectly symmetrical by Ryder (6, 384; 7, 329; 8, 787; 9, 727), but Jackson (11, 541; 12, 312) observed in his youngest spat that the lower left valve was larger and deeper than the upper right one.

A foot has been mentioned by Lacaze-Duthiers, Horst, Brooks and Jackson. Lacaze-Duthiers (1, 105) said: "En avant de l'anús un appendice pen saillant simule un rudiment de pied." Horst (2, 162) stated that "A foot-like prominence is developed, whereby the animal assumes some likeness to a young gastropod." Brooks (5, 53) wrote: "Near the center of the ventral surface—the top of Fig. 32—there is a well-marked and constant protuberance of the body wall, which occupies the region which, in most molluscan embryos, gives rise to the foot, and which may perhaps be regarded as a rudiment of that organ." In the same paragraph and referring to the same figure he mentions "the primitive digestive cavity" and on page 68 "the primitive digestive tract opens by a wide blastopore."

No one would claim that the part referred to in these extracts is the same organ as I have described in very much later larvæ. Referring to Horst's 1882 Fig. 6 or 1884 Fig. 10 we observe that it is only an accidental prominence, since it is bounded below by the invagination of the blastopore and above by that of the shell-gland, and further it disappears later on as in 1882 Fig. 10 or 1884 Fig. 14. Jackson (12, 302) affirmed: "The nearest approach to a foot known in the developing oyster is that shown in Fig. 24, p. 299 (after Horst), and I discovered no traces of a foot in my youngest specimens." The best that can be said about all references to a foot at these early stages is that, by comparison with other species, they indicate the place where, at a later date, through growth and specialization, a foot as well as several other parts are formed between the mouth and the anus.

"Otoceysts . . . here recorded so far as I am aware, for the first time," was written by McBride (14, 153), but a similar statement occurs in Lacaze-Duthiers of 1854 p. 1200, "Enfin j'ai vu apparaître les-otolithes . . . quelques globules agités de mouvements . . . dont personne n'avait même constaté l'existence." McBride's "Fig. 3. Larva of Oyster, six days old" shows two otoceysts, and in the near, right, one is a single otolith. There is something wrong about this. The oyster has about a dozen otoconia in each otoceyst, a fact which Lacaze-Duthiers was perhaps aware of when he wrote the words "quelques globules." If McBride's Fig. 3 properly represents his observations then it is not an oyster but a clam which I know to possess a single otolith in each otoceyst. Clams are very abundant along the beach immediately below where the station stood at Malpeque and it is a reasonable inference that this larva was taken up in the water used. On the same page occur the words "shell-gland . . . mistaken by Brooks for the gut." This was first pointed out by Horst in 1882.

Regarding the presence of a byssus Ryder (6, 383; 7, 329; 9, 758) was doubtful. Horst (3, 907) believed that he had noticed a small byssus. Jackson (12, 303) concludes that the oyster does not have a byssus at any period.

The absence of gills as well as the mention of symmetry in the following extract is only one of the indications that Ryder's (8, 787) conception of an oyster larva was constantly associated with the straight-hinge stage of the phylembryo: "One of the most conspicuous differences between the symmetrical larva and the young spat is the absence of gills in the former and their presence in the latter . . . two gill pouches . . . outer gill pouches."

Jackson (12, 303) studied the gills of the youngest spat stage and knew them to be the right and left innermost gills of the adult. He also mentions palps but says little about them. Jackson's study of the gills was so thorough and in general his observations were so exhaustive, considering the limited material, that it is worth while being cautious before suspecting him of an oversight, but I can not help thinking that what he took for palps was nothing but the foot. His figures (12, Figs. 1, 2) show it immediately behind the already shrunken velum and overlapped by the anterior gill-filaments. The two transverse lines may have been due to its being crumpled up, and the split towards the end of the ventral surface may have suggested two palps.

MONTREAL, Oct. 8, 1908.

## SHORTER ARTICLES AND CORRESPONDENCE

### SOME NOTES ON THE TRADITIONS OF THE NATIVES OF NORTHEASTERN SIBERIA ABOUT THE MAMMOTH

THE traditions of the Yukaghir very often mention the mammoth. They have a special name for him, *xolhut*. The spirit of the mammoth (*xólhut-áibi*—which means the mammoth's shadow), like the spirits of many other animals now living, appears in the rôle of a guardian spirit of certain shamans. A shaman assisted by the spirit or soul of a mammoth (*áibi* means shadow, spirit, and also soul) is regarded as the most powerful. According to this notion one might say that there was a time when the mammoth was a contemporary with man.

One Yukaghir tale relates to an episode in which the souls of two shamans (father and son) were riding on the back of a mammoth's shadow.

Another tradition tells of the disappearance of the mammoth. The creation of the mammoth was a blunder of the Superior Being. In creating such an enormous animal the Creator did not take into consideration the size of the earth and its resources. Our earth could not stand the weight of the mammoth and its vegetation was not sufficient to feed the mammoth race. The mammoth fed on tree trunks which he ground with his teeth, and in a short time the whole North of Siberia was deprived of trees. Hence is the origin of the northern tundra. In the beginning the earth had the form of an even plain, but by his weight the monster animal in moving about caused the formation of valleys and ravines in which rivers originated. In swampy or sandy places the mammoth sank into the ground and disappeared under the earth, where he froze during the winter. Often in the hole over him the water gathered into a lake. In this way the mammoth gradually disappeared from the earth's surface. This is why now whole cadavers of the animal are to be found in the frozen soil.

Among the Russianized Yukaghir of Nishnekolymsk I noted a tradition on the disappearance of the mammoth of a biblical

coloring. In the time of the flood Noah had to take besides the other animals a pair of mammoths. But when one of them put his fore legs on the raft he almost turned it over. Noah became terrified and quickly pushed his raft away from the monster. Thus all the mammoths perished.

Among the Chuckchee the mammoth is believed to be the reindeer of evil spirits. He lives underground and moves about through narrow passages. When a man sees a mammoth tusk protruding from the ground he must dig it up; otherwise the tusk will sink back into the ground. Once, it is said, some Chukchee found two mammoth's tusks protruding from the earth. They performed incantations and the mammoth came into sight. They lived on the mammoth for a whole winter.

A similar belief I found among the Tungus. On my way from the Okhotsk Sea to the Kolyma District over the Stanovoi Mountains I once spent a night on the banks of the lake "Kémennan" or the "Mammoth's Lake." Concerning the origin of this name I was told that some time ago a family of wandering Tungus encamped beside the lake. When they arose in the morning they saw two pair of mammoth tusks appearing from under the ice. The Tungus fled on their reindeer horror-stricken, from the lake, but they all died except one small boy in their next encampment.

It is interesting to note that in the languages of the above-mentioned tribes the mammoth ivory is called "mammoth horn" (*e. g.*, the Yukaghir call it "xólhut-ónmun," *i. e.*, horn or antler of the mammoth), and not tusk or tooth, as if the people of to-day have no proper conception of the appearance of the mammoth. On the other hand, the natives know that the Siberian mammoth had a thick hairy tail and the "horns" grew from the mouth.

The export of mammoth-ivory from Siberia is still considerable. From the northern part of the Yakutsk Province alone (in greater part from the New Siberia Islands) the Moscow market receives 1800 pud (*i. e.*, 64,800 English pounds) every year. The weight of a pair of tusks is from 200 to 500 pounds, with an average of 360 pounds. Hence the yearly exportation of ivory of the Yakutsk Province is equal to the tusks of 152 mammoths. When we take into consideration the period of 200 years since the exportation began we find that tusks of 25,400 mammoths were sent out of the Yakutsk Province. It must be added that

in former years the export was considerably greater than it is now.

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#### AGE OF TROTTING HORSE SIRES

THEORIES of heredity deduced from statistics always require critical examination. Statistics of heredity, like those of other subjects, offer striking possibilities to searchers for support of preconceived theories. I have recently completed some work with the trotting horse records, the result of which may be of interest inasmuch as it does not corroborate the results of other work in the same field.

Mr. C. L. Redfield has recently published a dynamic theory of development based largely on the statistics of the age of sires of average and of preeminent trotting horses. He assumes that by exercise a horse acquires "dynamic development," which facilitates speed and is transmitted. Dynamic development will naturally be greater in old than in young horses; in horses that are campaigned than in those not prepared for racing. Other things being equal, an old stallions' colts would inherit greater dynamic development and be faster than other colts sired by the same horse while younger. He found that the average trotting-bred horses, represented by the first one thousand animals listed in the Index Digest, were sired by stallions at an average age of 9.43 years. Representing the superior trotting horses by the 2.10 list, he based his calculations on the males appearing in four generations of each pedigree. The average time between generations in the male line in this instance was found to be 14 years; the sires were therefore practically 13 years old at the time of service. The difference between 9.43 and 13 years as the ages of sires of average and 2.10 horses is a very striking one and forms the basis of argument for the transmission of the dynamic development attributable to advanced age.

The matter of inheritance of dynamic development produced by racing, I propose to discuss at another time.

<sup>1</sup>Leader of the Riabouchinsky Expedition to Kamchatka, the Aleutian, Komandorski and Kurile Islands. Organized by the Imperial Russian Geographical Society. From 1900 connected with the Jesup North Pacific expeditions of the American Museum of Natural History. This contribution will be of very great interest both to ethnologists and zoologists.—H. F. O.

The following is from Mr. C. L. Redfield's recapitulation of his theory published in the *Horse World*, issue of February 27, 1906:

I said that I took one thousand registered stallions, alphabetically, from the *Index Digest* of the Register, and calculated the ages of their sires at the time when these registered stallions were foaled. From these I determined that the average time between generations in the male line was 10.43 years, which would give the average age of sires as 9.43 years at the time of service. I then said that, making all reasonable allowances for errors, the average time between generations in the male line might be set down as between 10 and 11 years, and that this period might be used as a standard in testing the age part of the theory. So far no one claims to have tested the accuracy of my calculation; no one claims that the figures I gave were wrong; and no one has said that these figures can not properly be used as a standard; yet if I am to be controverted, one of the first things to be done is to dispute the accuracy of my standard.

I then took the entire list of 2.10 trotters as an appropriate class of animals to be used in testing the inheritance of dynamic development, and I calculated the ages of their male progenitors for four generations. The number of animals involved was over five thousand and I gave the average time between generations in the male line for the production of 2.10 trotters as being approximately 14.00 years. This is an average of nearly 40 per cent. over the standard average determined from the Register, and my explanation of this remarkable difference was that it indicated the inheritance of acquired dynamic development. So far no one has disputed the accuracy of my computation and no one has attempted to give any other explanation of such an unusual divergence from the natural order of things.

Am I right or am I wrong? If I am wrong will some one please come forward with a better explanation.

It is to be noted that in the case of the average horses represented by the first thousand in the *Index Digest*, the ages of their *immediate* sires only were computed, and found to average 9.43 years; whereas in the case of the horses in the 2.10 list *all the sires appearing in the first four generations* were brought in. Assuming 14 years to be correct for the average time between generations, this carries us back 56 years.

The first horse that was uniformly successful as a sire of speed was Hambletonian 10 foaled in 1849. In the sixties this horse's reputation as a sire of speed was established and he did heavy stud service until the time of his death in 1873.

This was the real beginning of the trotting breed of horses. During the later years of the life of Hambletonian 10 and subsequent to his death his sons were patronized by owners of well-bred and speedy mares. The more successful of these sons naturally received heavy stud patronage as long as they remained serviceable. When the grandsons of Hambletonian 10, with two generations of speed-producing sires back of them and out of selected female ancestry, came into service, it was found that in many instances they sired faster colts than did their sires or grand sire. Only in more recent years were representatives of popular families used for stud purposes in earlier life.

In view of these facts, I deem it unfair to base a conclusion upon a comparison of two results, one of which (13 years as the average age at time of service of sires in four generations back of horses in the 2.10 list) comes largely from an investigation of the formative period of the breed, while the other (9.43 years as the average age at time of service of immediate sires of average horses) mainly refers to more recent conditions.

If the figures 9.43 and 13.00 had been derived by similar means their value would be unquestionable. A really fair comparison would demand the same procedure in one case as in the other. Either all sires in the four generations of the thousand horses should be used or else only the immediate sires of those in the 2.10 list.

Assuming 9.43 to be correct for the average age of the sires when they produced the first one thousand horses in the *Index Digest*, I have attempted to secure a similar figure for the immediate sires of the horses in the 2.10 trotting list as published in "Yearbook," Volume 22. The list published in that volume contains 279 horses. In thirty cases the records failed to show the horse's age. In seven cases the age of the sire is not given. This leaves 242 of the 279 in the list for which the ages are shown.

Below are given two extremes and the average for 242 horses regarding which there exists no uncertainty:

Horse	Foaled	Sire	Sire foaled	Age of Sire at Time of Service
Wentworth 2.04½	1903	Superior	1879	23.
Dolly Dillon 2.06½	1895	Sidney Dillon	1892	2.
Average for 242 horses				9.41

Of the 242 horses,

1	was sired by	2 year old stallion
11	were sired by	3 year old stallions
17	were sired by	4 year old stallions
30	were sired by	5 year old stallions
19	were sired by	6 year old stallions
21	were sired by	7 year old stallions
21	were sired by	8 year old stallions
25	were sired by	9 year old stallions
14	were sired by	10 year old stallions
17	were sired by	11 year old stallions
8	were sired by	12 year old stallions
13	were sired by	13 year old stallions
8	were sired by	14 year old stallions
9	were sired by	15 year old stallions
6	were sired by	16 year old stallions
6	were sired by	17 year old stallions
1	was sired by	18 year old stallion
4	were sired by	19 year old stallions
3	were sired by	20 year old stallions
0	were sired by	21 year old stallions
6	were sired by	22 year old stallions
2	were sired by	23 year old stallions

Taking 9.43 years as the average age of sires of average horses and substituting 14 by 9.41 years as the average age of sires of 2.10 trotting horses, it is evident that the records do not reveal any superiority of the old sire over the younger one.

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#### THE OCCURRENCE OF BATRACHOCEPS ATTENUATUS AND AUTODAX LUGUBRIS IN SOUTHERN CALIFORNIA

RECENTLY the salamander *Autodax lugubris* has been found near Los Angeles, Cal.<sup>1</sup> So far as I know, until this animal was reported no salamanders were known to live in southern California out from the mountains, although in the mountains and cañons of the foothills here and there as far as San Diego, another characteristic Pacific-coast salamander, *Diemyctylus*

<sup>1</sup> Miller, L. H., AM. NAT., Vol. XL, pp. 741-742.

*torosus*, has long been known. I have found it commonly in a number of cañons of the San Gabriel range and heard of it in other parts of southern California; in some places it seems to be quite abundant.

Two years ago last spring, just after the winter rains were over, a salamander was brought into the laboratory. It had been found in a garden near an orange orchard in Claremont, Cal., about four miles from permanent flowing water of the mountains and several hundred feet above subterranean water; the only water that could come to it was from rains and from irrigation. It was a full-grown specimen of *Batrachocephalus attenuatus*. Some weeks later in the early part of June another full-grown specimen was brought in from another locality near Claremont. This time it was from a large, dry, uncultivated area and was found under a stone. A few hundred feet from the place where it was found there was a deep well. I afterward learned that ten or more years earlier a pond of considerable extent had covered this place.

During the winter of 1906-7 two small salamanders were sent to me from San Diego. They were half-grown *B. attenuatus*. The identification of these four specimens extends the known range of this species some hundreds of miles.

In May of this year a number of other salamanders were obtained from well up in the mountains north of Claremont, a number of specimens of *B. attenuatus* and two full-grown specimens of *Autodax lugubris*. The specimens of *Autodax* were found in a narrow crevice in a high rocky wall. This sort of a location is quite different from the other places where *Autodax* has been found.

Judging from the character of the land and water of Lower California it seems quite probable that one or all of the species mentioned in this note may occur farther south than San Diego.

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## NOTES AND LITERATURE

### EXPERIMENTAL EVOLUTION

**The Effect of the Environment upon Animals.**—The second volume of Bachmetjew's great work, "Experimentelle Entomologische Studien" (1), will be welcomed by all who are interested in the effect of external factors upon organisms. It will doubtless surprise many that, although dealing almost exclusively with insects, the author reviews more than 1,200 papers. Even so, seasonal dimorphism, protective coloration mimicry and parthenogenesis are only touched upon incidentally as it is intended to take them up in a later volume. Furthermore, practically none of the literature since 1905 is included. The first 600 pages of the book are taken up with short abstracts arranged in chronological order within appropriate groupings. These abstracts are then rearranged—often being repeated verbatim—in the "theoretical part" according to their bearing upon special problems. Although the author states his opinions concerning the significance of the data thus brought together, the reader is largely left to draw his own deductions, as it seems to have been the aim of the author to make a handbook to the literature of experimental entomology rather than a dissertation in support of his own views. There can be little room for doubt in view of this immense amount of evidence that environmental factors are responsible for many—perhaps most—of the variations and aberrations among insects. However, there is, as yet, little proof that they produce heritable modifications such as we believe real species to be made of. In this regard Tower's work with *Leptinotarsa* is a remarkable exception. Practically all the results so far obtained, while interesting and important, belong to physiology rather than to evolution.

Federly is continuing his work concerning the effect of external conditions upon the scales of Lepidoptera. A recent paper (2) reviews the literature of albinism and gives certain original observations. True albinism seems to be rare. However, cases of "pseudo-albinism," due to a reduction in the size of the scales but not in the intensity of the pigment nor in the number of

pigment-bearing scales, are fairly common. This condition probably arises through an inhibiting action of the environment upon the "scale mother cells."

An interesting case of an environmental effect which is not easily reversed is given by Marchal (3). *Lecanium corni*, a scale insect, becomes *L. robiniarum* when reared upon *Robinia pseudo-acacia* instead of its normal food plants, but the reverse experiment does not succeed.

Salamanders are a close second to insects as favorite material for the experimental study of the effects of the environment. Powers has contributed a valuable paper (4) on the causes of variation in *Amblystoma tigrinum* and promises proof that certain of these are inherited or at least perpetuated by reason of inheritance. Differences in the amount and character of the food produce remarkable modifications in the structure of the animal. If, as is hinted, variations in the appetite are inherited, we should have an interesting case of indirect transmission of characters. Among the conclusions the author says:

"Specific characters, in species which vary as *A. tigrinum* varies, are, after all, strongly determined by environing conditions. There is nothing new in this. But the study of this species seems to me to lend it new weight and confirmation. If the broad head and large teeth of the cannibal are acquired characters—and they conform to the definition of such—what are the narrow head and smaller teeth of the customary daphnid-feeder? Are these specific and congenital characters? They are more frequent, more "typical" in the species, but I am forced to conclude that they are so chiefly because daphnids are numerous and constitute a convenient and stimulating food. And the same may be said of nearly all specific characters; so readily are they modified by a changed environment that we must conclude they are, in reality, equally determined even by an unchanged environment. Congenital tendencies in such species are not definitely specific, but only indefinitely specific. In this species, indeed, they are not always even definitely generic."

Mr. Powers naturally points out that many of our catalogued "species" are merely ontogenetic and believes that "the zoologist must soon admit that the final test of many species must lie in the rearing, and that, too, under controlled conditions." We may, perhaps, go further and say that this is the test of all species, but that it is not worth while to apply the test in all cases. It is probably true that many of our so-called species are not orthodox species but are the results of reversible physiological

changes in the soma. However, they are the species as we have them and it seems a hopeless task to go through the animal kingdom and sort the named forms into "ontogenetic" species and "orthodox" species. We shall probably be forced to recognize that the names we give are merely convenient shorthand descriptions of certain organisms, some of which are extremely stable as to form and coloration, others not so much so. Our problem is, then, to find out as much as we can about the causes which bring about the differences which we note.

A new journal, *Zeitschrift für Induktive Abstammungs- und Vererbungslehre*, has just been started. With Baur, Correns and other authorities as editors, much is to be expected of it.

FRANK E. LUTZ.

#### LITERATURE

1. 1907. Bachmetjew, P. Experimentelle Entomologische Studien vom physikalisch-chemischen Standpunkt aus. Zweiter Band. Einfluss der äussern Faktoren auf Insekten. xevi + 944 pp. with 25 plates. Sophia.
2. 1908. Federley, Harry. Über den Albinismus bei den Lepidopteren. *Acta Societatis pro Fauna et Flora Fennica*, XXXI, No. 4.
3. 1908. Marchal, P. Comptes rendus Soc. de Biologie, July. LXV, No. 24.
4. 1907. Powers, J. H. Morphological Variation and its Causes in *Amblystoma tigrinum*. *Studies from the Zoological Laboratory, the University of Nebraska*, No. 71. 77 pages with 9 plates.

#### EXPERIMENTAL ZOOLOGY

**The Influence of the Size of the Egg and Temperature on the Growth of the Frog.**<sup>1</sup>—What determines the difference in size of two animals? It is the difference due to greater or less number of cells, or, perhaps, to a difference in the size of their cells? Does the animal grow by adding more new cells, or by increasing the old cells? These are some of the problems which confront the student of the phenomenon of growth in the animal and plant kingdom alike.

The paper, the subject of this review, contains an account of experiments which attempt to throw light upon these problems.

<sup>1</sup> Einfluss der Eigrösse und der Temperatur auf das Wachsthum und die Grösse des Frosches und dessen Zellen. Von Robert Chambers, *Arch. für Mikroskopische Anatomie und Entwicklungsgeschichte*, Vol. 72, Part 3, pp. 607-661, 1908.

Chambers experimented with eggs of *Rana temporaria* and *R. esculenta*, and his object was to determine how the initial size of the eggs and temperature affect the size of developing embryos. He found that the eggs of both species show considerable variations in size, that are in no way connected with the prevailing temperature of the locality from which those eggs are collected. The average size of eggs varies not only with the species or locality, but also with each individual frog. Furthermore, eggs laid by one frog also present variations in size, which, in one case, were 1.8 mm., 1.2 mm., 1.15 mm., and 1.05 mm. in diameter. The eggs measuring 1.15–1.20 mm. were most abundant.

Contrary to what one might expect, there is no relation between the size of frogs and the size of eggs which they lay, and small frogs with large eggs as well as large frogs with small eggs are frequently found.

In the first place Chambers undertook to determine the relation of the size of an egg to the rate of its development and subsequent growth of the embryo. He divided eggs of a single frog into lots according to their sizes, and found, on rearing those, that small eggs have a tendency to develop slightly faster than large eggs. This tendency is marked only in the early stages, for as the tadpoles commence to feed those developing from large eggs grow faster and pass through metamorphosis sooner.<sup>2</sup> On rearing eggs of two lots, one containing eggs of large and uniform size, the other containing eggs of various sizes, it was found that the size of tadpoles varied considerably in favor of the former. Besides, the tadpoles of the first lot have all metamorphosed in course of two weeks, while two months have elapsed before the tadpoles of the second lot had all metamorphosed. There is one point in connection with this experiment on which unfortunately Chambers gives no information, and yet it may alter the conclusion drawn from the experiment. He mentions that there were 70 eggs in the first lot and 100 eggs in the second lot. If the eggs of both lots were distributed in an equal number of dishes there must have been fewer eggs of the large size than of the mixed sizes to each dish. The difference in the rate of development and in the size of tadpoles might have been therefore caused by the more or less crowded condition of the eggs, and not by the large or small initial size of the eggs. In fact, Chambers resorts to this factor of the number of eggs de-

<sup>2</sup> See page 7.

veloping in a dish to account for the fact that in experiment with eggs of 1.81 mm. and 1.20 mm. in diameter, the eggs of both sizes developed equally fast. The less crowded condition, he thought, compensated in that case for the small size of the eggs. The question as to whether or not the initial size of the egg is a determining factor in the rate of development seems to me, therefore, still an open question.

Next, Chambers investigated the influence of the size of the eggs upon development at different temperatures. Eggs of *R. temporaria* of the same size were reared separately under temperatures ranging from 10° to 25° C. He found in this case of *R. temporaria*, which spawns early in the spring, that both large and small eggs develop at low temperatures, but only the large eggs are capable of resisting higher temperatures. On the contrary, in case of *R. esculenta*, which spawns in May and June, all eggs develop well at high temperature (19°–27° C.) and only the large eggs develop at low temperature (10°–12° C.). Chambers therefore concludes that large eggs are more efficient in withstanding extremes of temperature.

He found, furthermore, that when eggs of the same individual are reared, under equal conditions of temperature, eggs larger or slightly smaller than those of normal size (the size of the majority of eggs is considered the normal size) develop to advanced stages, but the extremely small eggs invariably die out while yet in the early stages of development. In a lot of eggs, where the normal size was 1.5 mm. only 8 out of 23 eggs measuring 1.15 mm. in diameter and none of those measuring 1.05 mm. reached an advanced stage. Chambers is strongly inclined to think that there is a set limit to the size of the egg of a given species, beyond which it can no longer vary without losing its power of development. But the failure of abnormally small eggs to develop can also be interpreted differently, since the exceptionally small size may be due to the circumstance that the eggs have not yet attained full maturity.

Chambers states that large tadpoles develop always from large eggs, and that the ratio between the volumes of different eggs is maintained more or less constant during the early stages of development, i. e., the tadpoles are in the same relation to each other, as regards volume, as the eggs from which they have developed.

Regarding the cellular elements of the young developed from

large or small eggs, Chambers found from his study of sections of various organs and tissues (lens, ear-vesicle, rectum, epidermis, cartilage, muscle-fibers and blood-corpuscles), that the size of the cells of a tadpole or young frog is in direct relation to the size of the examined individual. This in general agrees with the results from my own work, which I hope to publish in the near future, on the cells of large and small salamanders.

Since, as was shown above, the size of the embryo depends upon the size of the egg from which it develops, Chambers draws the further conclusion that the size of cells of an animal is determined by the initial size of the egg from which it has developed.

In another experiment, where eggs of *R. temporaria* were reared at two temperatures of 10° and 25° C., the tadpoles of the first set (10° C.) metamorphosed two months later than those of the second set (25° C.), but the young frogs developed in the medium with a low temperature (10°) were fully one and one half times as large as those developed at a higher temperature. Whether this large size was due to the low temperature or to the fact that the tadpoles had been growing two months longer before metamorphosing, this point is not made clear. However, on examining cells from the epidermis and rectum Chambers found that the differences in total size of frogs, developed at a high or a low temperature, extend also to their cells, so that large specimens have correspondingly larger cells than small specimens.

But the initial size of the eggs and the temperature of the medium are not the only factors determining the size of the tadpoles and young frogs, because large and small individuals may develop even from eggs of uniform size and under similar conditions of temperature. What has been found in regard to the variations in size of the eggs may of course be also true in case of the sperms, which might thus be a factor determining the size of the young. At any rate, Chambers made an interesting observation that tadpoles developed from eggs of the same size begin to vary only after the supply of yolk has been exhausted and they have commenced to take in food. It is not improbable, therefore, that the variations in size result either from an insufficient amount of food available for some tadpoles, as is the case, for instance, in growing starfishes,<sup>3</sup> or else the tadpoles may consume unequal amounts of food under different conditions of health.

<sup>3</sup> Mead, A. D. On the Correlation between Growth and Food-supply in Starfish. AMER. NAT., Vol. 34, No. 397, pp. 17-23, 1900.

It is a matter of some interest that Chambers maintains that the cells of large and small individuals developed from eggs of uniform diameter are not of different but of the same size. Thus he leads us to believe, and in fact he states it explicitly at the close of his paper, that the principal factor determining the size of cells of an animal is the initial size of the egg from which it developed.

Without giving mention to some objections to this general conclusion, which might be made on the basis of Chambers' own experiments, I wish to point out that the figures of cells given in the text do not carry conviction, and, so far as I was able to make out, they do not bear out Chambers' contention. In the drawings of cells of blood-corpuscles, epidermis and rectum, which Chambers thinks to be of equal size, I find on careful examination that the cells are different. Of course, actual measurements of the cells could make this matter clear, but, unfortunately, there are no measurements given in the paper.

The introduction to the paper contains a résumé of a few works in one way or another related to the problem. This résumé of facts so widely scattered throughout the literature will doubtless be found useful.

The third part of the paper is devoted chiefly to extensive theoretical considerations and does not therefore come within the scope of the present review.

In conclusion I should like to call attention to some defects of a technical character, which obscure the meaning of the text and frequently confuse the reader. In the explanation to Fig. 1 it is said, for instance, that I marks a culture developed from eggs of similar size, and II marks those developed from eggs of different and not ascertained sizes. But in the text referring to this Fig. 1 it is said that "Kulture II wurde mit Eiern angefangen, welche von gleicher, ausgesuchten Grösse waren." Which of these data, whether those found in the text or in the explanation to the figure, are the correct ones the reader is at loss to know, while the understanding of this point is important. On p. 635 we find reference to Fig. "A" and Aa in text Fig. 2. As a matter of fact this reference was found to apply to Fig. a and a<sup>a</sup> in the Text-fig. 5. In Table V in the third column the date of spawning is given as June 5, and the date of the first examination of the developing embryos is June 3.

There is, however, a more vital contradiction in the text. On p. 620 in a discussion of the facts presented in Table I we read: "Die kleineren Eier zeigten eine geringe Neigung sich schneller zu entwickeln." On p. 647 referring again to the Table I we read: "In den Furchungs- und Gastrula-Stadien zeigen die kleinen Eier die Tendenz, sich wenigerschnell zu entwickeln, als die grösseren Eier." And further on, p. 647, and referring again to the Table I, we read: "Da wir nun aber gesehen haben, dass die grossen und kleinen Eier sich gleichgut und gleichrash entwickeln (s. Tabelle 1) etc."

Thus it appears that the small eggs develop somewhat faster, and slower than the large eggs, and just as well as the large eggs!

SERGIUS MORGULIS.

#### PARASITOLOGY

**Cestodes of Birds.**—Fuhrmann has recently published (*Zool. Jahrb.*, Suppl. 10, Heft 1) a most valuable monograph on the Cestodes of Birds. He had at his disposal all the material from the great European museums and from the private collections of prominent European helminthologists, so that the work is vastly more valuable than a mere literary revision with studies on limited personal collections. In 1782 Goëze described 14 species of *Tænia* from birds; in 1819 Rudo'phi listed 54 certain and 30 uncertain species, and in 1850 Diesing recorded 81 certain and 28 questionable species. Von Linstow's *Compendium der Helminthologie* and *Nachtrag* in 1889 gave references to 230 bird cestodes from 340 host species. In this investigation Fuhrmann had material from 200 more species of birds at his disposal and recorded in all some 500 cestode parasites from them. When one considers that 12,000 species of birds are known and Cestodes have been collected from 540 only, it is clear that many more new forms are to be expected; these are to come most prominently from extra-European lands. North America which Fuhrmann notes as relatively unexplored, will contribute its share and I may add that investigations in this field are already in finished manuscript as studies from my own laboratory.

Some of the general conclusions which Fuhrmann has reached as a result of his 12 years of work in this field are of wide interest. The distribution of cestodes among the various group of birds shows that a given species occurs only in a given group

of birds and hence is typical of it. Birds with similar food habits shelter often radically different cestode parasites both in species and in genera. On the other hand, related birds of different food habits often show similar genera among their cestode guests even though the species differ. A zoogeographic survey of the cestodes in the various groups of birds shows a sharp contrast between the species found in different regions and furnishes strong evidence of the value of parasites as aids in zoogeographic investigations. In this respect the cestodes are unquestionably of the greatest value in the light of Fuhrmann's studies.

It would be impossible to abstract the systematic portion of Fuhrmann's paper. Many of the doubtful and insufficiently described species of other authors are here positively evaluated after comparison of the original material. Each genus is characterized on the basis of the author's investigations and the type species designated. The other species are also listed with references to the appropriate literature and to all known hosts. The faunistic section contains a complete list of the hosts with their cestode parasites and a record of the geographic distribution. A good alphabetic index of families, genera, species and synonyms, together with a full bibliography, closes the paper. Though not stated specifically, the monograph appears to be confined to the Cyclophyllidea and all will await with great interest the publication by this author of further studies dealing with other groups of avian cestodes.

A paper by Plehn (*Zool. Anz.*, 33: 427) on a blood-inhabiting cestode designated *Sanguinicola*, is of especial interest both from the morphological and from the biological standpoint. The animal occurs in the blood system of Cyprinid fishes, being most frequently found in the *bulbus arteriosus*, and was originally described in 1905 as an aberrant rhabdocœl. In structure it agrees well with the few monozoic cestodes classed together as *Cestodaria* and often separated from other cestodes. The species does not reach full development in this host, or at least in the blood vessels, since no specimens with fully developed female organs have yet been found. The author conjectures that it is withdrawn by some blood-sucking parasite and undergoes further development in that host. In view of the size of the worm and its evident inability to reach even the superficial arterioles, such a life cycle seems at least unlikely. The confessedly imperfect account of the structure of this worm makes any dis-

cussion of its precise genetic relationships unwise and the proposed phylogeny of parasitic flatworms based upon it has therefore only a purely suggestive value.

The Harben lectures for 1908, which were delivered by Professor George H. F. Nuttall, of Cambridge, England, have been printed (*Jour. Roy. Inst. Pub. Health*, July-September, 1908). The topics covered are the ticks and the diseases which they transmit to man and domestic animals; the diseases are among the most important of those caused by animal parasites especially and are due to spirochaetes, piroplasma and filaria. Nuttall's account, which is the most complete résumé available in this field, is notably lucid and scholarly in presentation.

HENRY B. WARD.

